

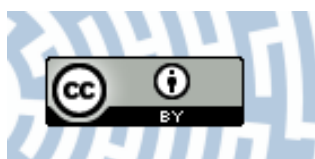


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# Late Frasnian Atrypida (Brachiopoda) from Poland and the Frasnian-Famennian biotic crisis

GRZEGORZ RACKI & ANDRZEJ BALIŃSKI



Racki, G. & Baliński, A. 1998. Late Frasnian Atrypida (Brachiopoda) from Poland and the Frasnian-Famennian biotic crisis. — *Acta Palaeontologica Polonica* **43**, 2, 273–304.

Late Frasnian Atrypida (Brachiopoda) from the Holy Cross Mountains, Poland, include 15 taxa and were widely distributed in foreslope habitats of the declining Dyminy Reef complex. The *Palmatolepis semichatovae* transgression, followed by the transgressive/hypoxic Lower Kellwasser (KW) Event during the *Palmatolepis rhenana* Zone did not have catastrophic effects for atrypid faunas, but were rather associated with the appearance of a new species group comprising *Iowatrypa*, *Waiotrypa*, *Costatrypa*, *Spinatrypina*, *Desquamatia* and *Radiatrypa*. Stepdown demise of the biota started during the inter-KW regression, and culminated as a result of increasing stress during the Upper Kellwasser Event in the late *Palmatolepis linguiformis* Zone, mainly due to catastrophic sea level changes and anoxia, possibly linked to oceanic thermal changes (cooling) and nutrification pulses. The extinction pattern was diachronous and facies-controlled in this area, and the last atrypid survivors reached the Frasnian-Famennian (F-F) boundary. Increasing expansion from the adjacent deeper-water environment of the more resistant assemblages, with productids, cyrtospiriferids, athyridids and schizophoriids, occurred in the final crisis interval. This brachiopod fauna profusion characterized the earliest Famennian survival and early recovery phases of the mass extinction in this part of the Laurussian shelf, as well as the continuity of the deeper-water rhynchonellid-inarticulate biofacies across the F-F boundary. *Spinatrypina* (*Exatrypa*) *relicta* sp. n. is proposed as new.

**Key words:** Brachiopoda, Atrypida, taxonomy, biostratigraphy, palaeoecology, mass extinction, Kellwasser Crisis, Frasnian, Famennian, Devonian, Poland.

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## Introduction

Exposures in the Holy Cross Mountains, Central Poland (Fig. 1), have been palaeontologically and biostratigraphically studied since the second half of the 19th century, but knowledge of the late Frasnian brachiopod faunas is still limited, with the exception of gypidulids (Godefroid & Racki 1990) and athyridids (Baliński 1995b; Grunt & Racki 1998). This is especially true for common Atrypida, the stratigraphically older

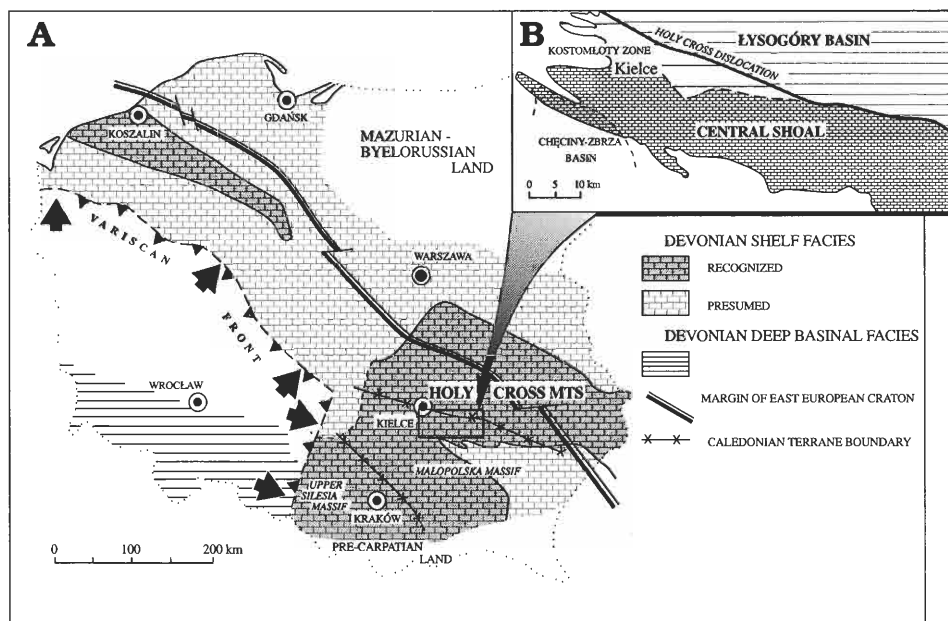


Fig. 1. **A.** Location of Holy Cross Mountains against the palaeogeographic and structural framework of the Devonian in Poland (compiled after Matyja & Narkiewicz 1992: fig. 1, and Dadlez *et al.* 1994: fig. 1). **B.** Palaeogeographic plan of the Devonian of Holy Cross Mountains, essentially for the Givetian to Frasnian time interval (based on Racki 1993b: fig. 2).

of which, chiefly Middle Devonian taxa, were described by Biernat (1964, 1971), Racki & Baliński (1981), and Racki (1993a). Atrypid brachiopods, the principal component of the Devonian reef-related shelly benthos (Atrypid–Gypidulid Biofacies of Racki *et al.* 1993), totally collapsed near the Frasnian–Famennian (F–F) boundary during the global biotic crisis, as is well recorded in the Holy Cross Mountains (e.g., Narkiewicz & Hoffman 1989; Racki *et al.* 1989; Racki 1990).

The taxonomic study of the late Frasnian Atrypida is an important step towards the understanding of the profound brachiopod turnover during the F–F ecosystem catastrophe. The Holy Cross fauna characterized a distinctive (decline) segment of the Middle–Upper Devonian, backstepping bank-to-reef complex evolution (see Figs 2–4). The key late Frasnian brachiopod aspects are linked to the questionable record of the anoxic Kellwasser (KW) Events and KW Crisis (*sensu* Schindler 1990; see also Walliser 1996) in this fragment of the Laurussian shelf region (Racki 1993b, 1993c, 1996; Sartenauer *et al.* 1998). Accurate estimation of the stratigraphic range of atrypid taxa enabled revision of disputable occurrences of the last atrypids in the Famennian (Biernat 1970), which is one of the crucial faunal problems relating to this biotic crisis (Copper 1986).

## General structural and paleogeographic setting

The Devonian strata of the Holy Cross Mountains belong to the elongated belt between the southwestern margin of the East European Craton and the Variscan Deformation

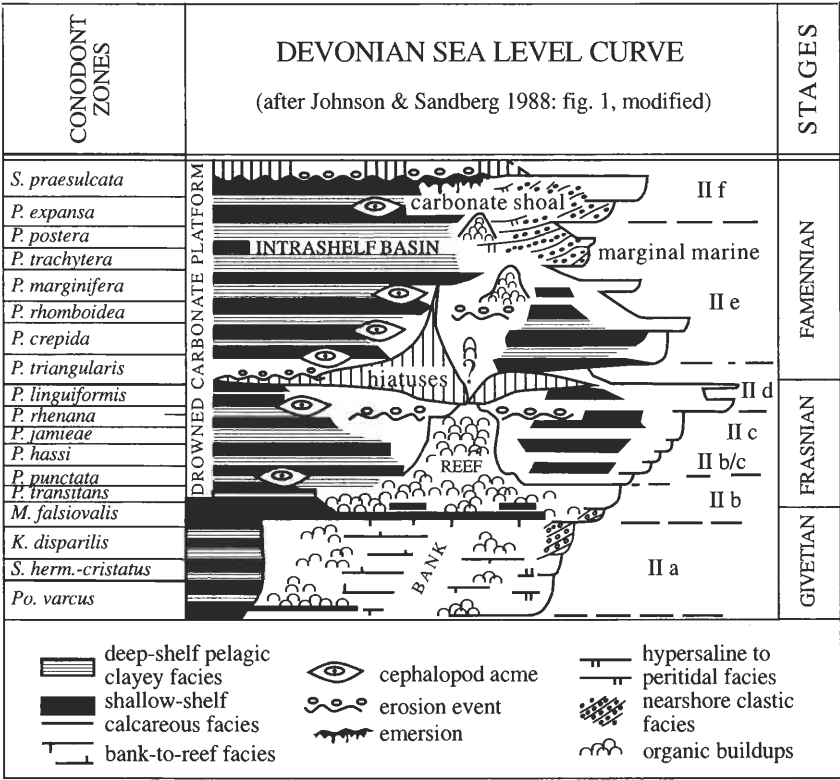


Fig. 2. Eustatic framework of Late Devonian in South Poland (after Racki 1997). Abbreviations of generic names: *S.* – *Siphonodella*, *P.* – *Palmatolepis*, *M.* – *Mesotaxis*, *K.* *Klapperina*, *Po.* – *Polygnathus*, *S.* – *Schmidtognathus*.

Front (Fig. 1A), delineating the controversial extent of the Wielkopolska and Silesian–Moravian Variscides, as summarized by Dadlez *et al.* (1994). The Devonian overlap sequence developed over both fragments of the Caledonian marginal fold-and-thrust zone and two possible terranes, the proximal Małopolska Block and the exotic(?) Upper Silesia Block.

The carbonate shelf, up to 600 km wide, formed the Polish fragment of a pericratonic basin stretching from the western margins of Europe to the Ukraine, along the periphery of the ‘Old Red Sandstone Continent’ (Laurussia). The southern part of the basin, extending to the Moravian Karst and Pre-Carpathian Land (Fig. 1A), is best known from numerous outcrops in the Holy Cross Mountains and the Silesia–Cracow area, as well as from boreholes. Two distinct palaeogeographic-tectonic regions of the Holy Cross area (the Kielce palaeohigh and Łysogóry palaeolow; see Fig. 1B) offer an opportunity to compare the brachiopod record across the F–F boundary in differing sedimentary facies (Fig. 3). A subsymmetric facies plan is emphasized in the central location of the Frasnian Dyminy Reef, and a Famennian remnant pelagic ridge was surrounded by expanding intrashelf basins with Chęciny–Zbrza to the south and Łysogóry–Kostomłoty to the north (see Szulczewski 1995 for summary). The southern closure of the epeiric sea was formed mostly by the postulated Pre-Carpathian Land (Narkiewicz 1988). The Zawiercie–Dęb-

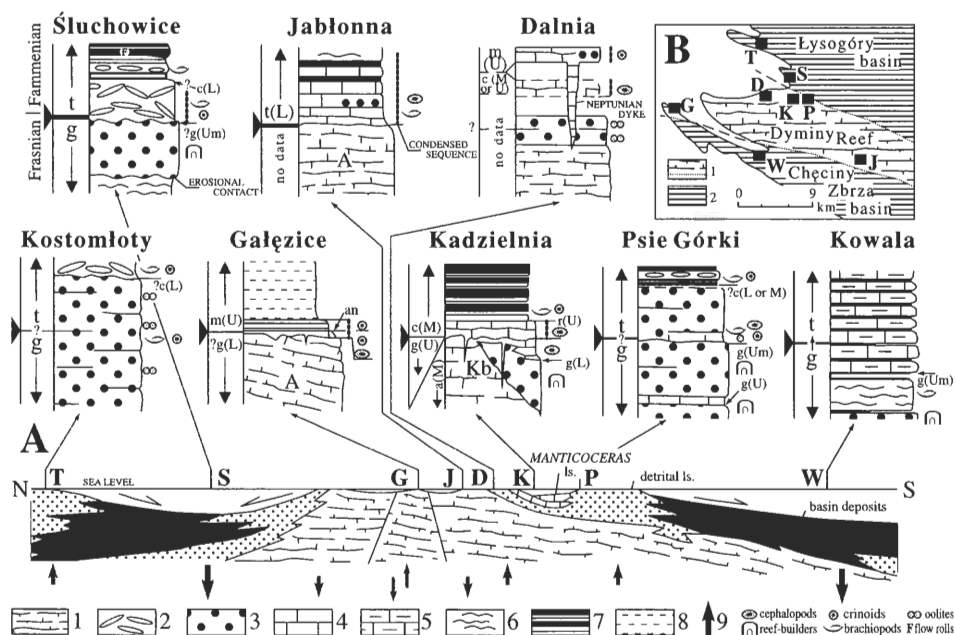


Fig. 3. Paleogeographic setting of the Frasnian–Famennian transition in the western Holy Cross Mountains (after Racki 1990: fig. 4, modified). **A.** Key profiles presenting particular facies settings (thickness not to scale); schematic cross-section adopted from Szulczewski (1971: fig. 11C). Conodont dating of facies changes (arrowed): a – *Polygnathus asymmetricus*, g – *Palmatolepis gigas* (Um – *Palmatolepis linguiformis*), t – *Palmatolepis triangularis*, c – *Palmatolepis crepida*, r – *Palmatolepis rhomboidea*, m – *Palmatolepis marginifera*, an – *Scoliognathus anchoralis*, L – Lower, M – Middle, U – Upper; interval of dating uncertainty is marked by thickness of separating line at the F–F boundary; 1 – stromatoporoid-coral biolithites (A – *Amphipora*-limestones, Kb – Kadzielnia-type bioherm), 2 – flat-pebble conglomerates, 3 – other detrital limestones, largely intrabiorudites, 4 – micrites, 5 – medium-bedded marly to micritic limestones, 6 – nodular marly deposits, 7 – interbedded marly limestones and shales, 8 – cherty shales, 9 – subsidence or uplift (length of arrow corresponds to relative rate of displacement). **B.** Paleogeographic scheme with location of sections from **A**; 1 – reef-limestones rimmed by detrital (slope) deposits and succeeded by condensed cover with hiatuses, 2 – generally argillaceous (basin) deposits, D – Dálnia, G – Gałęzice, J – Jablonna, K – Kowala, P – Psie Górki, S – Sluchowice, T – Kostomłoty, W – Kowala.

nik cross-section is situated at the northeastern periphery of the stable Upper Silesian Block, in the zone of a Caledonian suture (see Dadlez *et al.* 1994). The Late Devonian brachiopod sequence has been described at Dębnik near Kraków (Baliński 1979, 1995a), and has been used here as a comparative atrypid succession for this study.

## Facies and eustatic framework of the Frasnian–Famennian transition

A eustatic framework for Late Devonian sedimentation in the area is requisite to the recognition of biotic events (Narkiewicz 1988; Racki 1993b, 1993c; Baliński 1995a). The F–F passage beds have been dated with conodonts in most of the Holy Cross Mountains sections, and in other Polish successions (see summary in Racki & Turnau

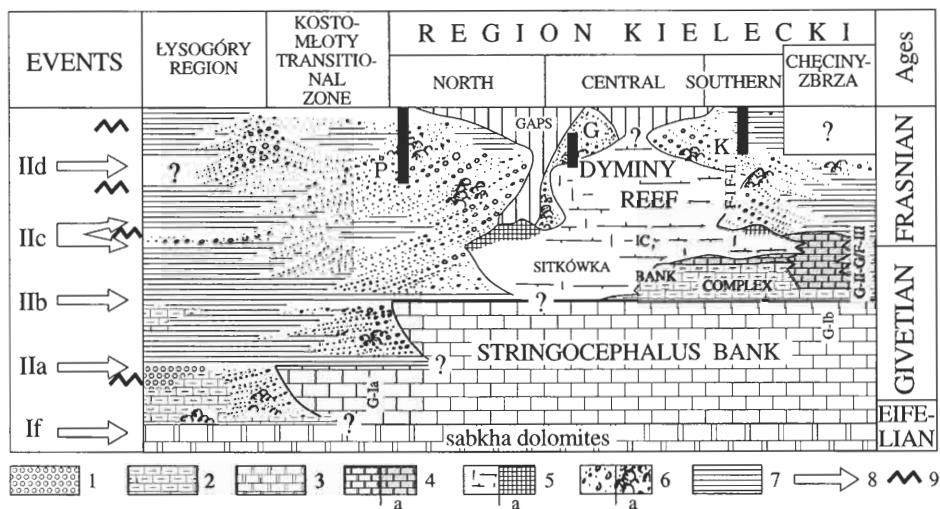


Fig. 4. Position of the main atrypid-bearing sections under study (K – Kowala-Łgawa Hill, arrowed; G – Grabina, P – Psie Górki) against developmental stages of the Devonian bank-to-reef complex of the Holy Cross Mountains; stratigraphic-facies cross-section (after Racki 1993b: fig. 3, changed) is shown to emphasize eustatic rhythmic control of the depositional pattern; Ie–IId – Transgressive–Regressive (T–R) Cycles modified from Johnson *et al.* (1985), G–Ia to F–II – regional sedimentary units (Racki 1993b). 1 – siliciclastics; 2 – marls and limestones; 3 – dolomites (secondary dolomitisation omitted); 4 – biostromal bank facies (a – intershoal facies); 5 – reef facies (a – Kadzielnia-type bioherms); 6 – carbonate slope facies (a – organic buildups); 7 – marly limestones and shales (basin facies); 8 – main transgressive events; 9 – synsedimentary tectonic episodes.

in press). Taxonomic refinement of the conodont index species (*Palmatolepis prae-triangularis*–*P. triangularis* transition; see Sandberg *et al.* 1988) is necessary, however.

The Late Devonian carbonate shelf succession indicates continuous, but punctuated, drowning of an increasingly differentiated carbonate platform, finally completed in the Viséan (Szulczewski 1995). The recognized events (see Racki in press) coincide overall with the Euramerican sea-level curve of Johnson *et al.* (1985), arranged in the successive Transgressive–Regressive (T–R) Cycles (Fig. 2). The last developmental phase of the carbonate complex included growth of isolated reefs (Figs 3, 4), exemplified by the Dyminy Reef in the Holy Cross area (Racki 1993b). Cessation of reef development, combined with the widespread onset of hypoxia are attributed to the late Frasnian IId T–R Cycle and Lower KW Event. This marked the carbonate platform demise and the beginning of basinal sedimentation, accelerated during a sustained, stepwise, early Famennian (Ile) sea-level rise. In addition, Narkiewicz (1988), Narkiewicz & Hoffman (1989) and Racki (1995) discussed the evidence for a regressive eustatic event in the Lower *Palmatolepis gigas* Zone (= Early *Palmatolepis rhenana* Zone; see Ziegler & Sandberg 1990). Broad distribution of intensive intraformational erosion is suggestive of block movements over this part of the Laurussian shelf (Racki 1993b), probably linked with the initiation of rifting in the Prypyat–Donets–Dnieper Trough (see Racki in press).

The signature of rapid eustatic movements in the F–F transition is also strongly biased by synsedimentary tectonics, including block tilting and emersion (e.g., Szul-

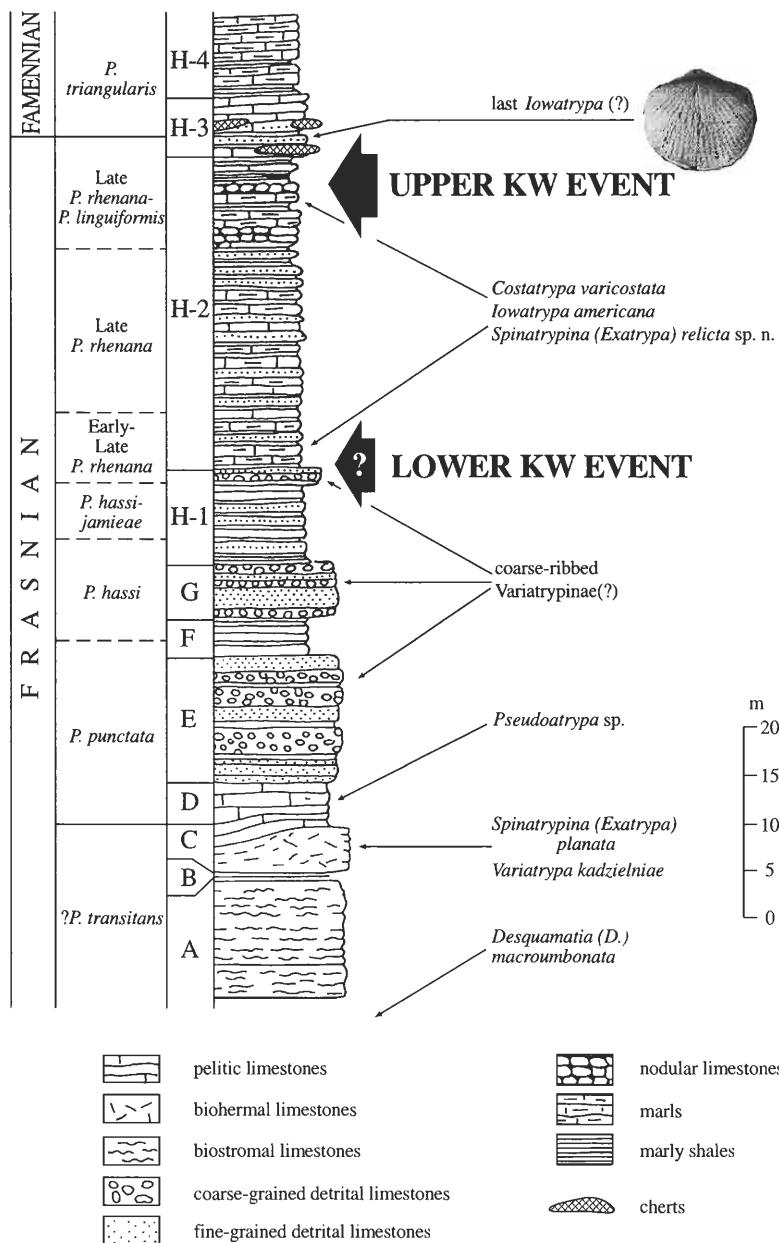


Fig. 5. Composite lithologic section of the Frasnian to early Famennian, limestone to marly succession at Kowala – Łgawa Hill, based on the Kowala railroad cut (Szulczewski 1971: fig. 7) and western walls of the quarry, and simplified distribution scheme of the atrypid assemblages against supposed levels of the Kellwasser transgressive/anoxic events in the late Frasnian sea-level highstand (Schindler 1990; Sandberg *et al.* 1992). Set terminology after Szulczewski (1971: p. 75), with new subdivision of the set H, and revised conodont datings (see also Racki 1993b, 1993c). Note, that unit H-2 reveals pronounced lateral variability into more nodular varieties.

czewski 1971; Szulczewski *et al.* 1996). This tectonic rejuvenation pulse might be a regional echo of worldwide processes that are presumed by Racki (in press) to have been an important trigger of the F-F ecosystem collapse. Furthermore, a loss of carbonate production occurred near the F-F boundary, manifested in common hiatuses and condensations (Narkiewicz & Hoffman 1989; Matyja & Narkiewicz 1992), especially on the top of suppressed reefs (e.g., at Kadzielnia; Szulczewski 1971). Consequently, the *Palmatolepis linguiformis* Zone was frequently not documented, while the Early *Palmatolepis triangularis* Zone was at least conspicuously reduced in thickness, even in the most complete downslope to basinal sequences (see Fig. 3). A marked sea-level drop in the late *Palmatolepis linguiformis* Zone (e.g., Sandberg *et al.* 1988, 1992) is recorded in a calcareous-bioclastic episode interrupting rhythmic clayey-marly deposition (Racki 1993c, in press; see also Matyja & Narkiewicz 1992).

The material described here is housed at Department of Earth Sciences, Silesian University in Sosnowiec (abbreviated GIUS 4).

## Systematic palaeontology

The atrypid collection under study comprises more than 400 specimens, variously preserved. Most significant are the silicified faunas from the micritic-marly lithologies of Jaźwica and Kowala (Figs 4, 5; see Appendix 1). Material from reef-related limestone sequences (e.g., Psie Górki, Kadzielnia, Wietrznia, Miedzianka) is preserved chiefly as single and exfoliated valves, and the brachiopod nest-like accumulations from Grabina and Tudorów are exceptions. However, the common fibrous-calcite filling is coupled with recrystallization of the shell interior and the almost complete obliteration of the internal morphological characters (as in the Kadzielnia bioherm fauna; see Biernat 1971).

**Abbreviations:** L – length of the shell (= length of the pedicle valve), Ldv – length of the brachial valve, W – width of shell, S shell size ( $L + W/2$ ), T – thickness of shell, Tv – thickness of the pedicle valve, Wh – width of hinge, Nr – total number of ribs, R-5 – number of ribs per 5 mm near anterior shell margin.

Family Atrypidae Gill, 1871

Subfamily Atrypinae Gill, 1871

Genus *Costatrypa* Copper, 1973

**Remarks.** — The definition of *Costatrypa* follows Cooper & Dutro (1982) and Copper & Racheboeuf (1985), in accordance with the stratigraphic differentiation between the Early–Middle Devonian *Atryparia* and the Frasnian *Costatrypa*.

*Costatrypa varicostata* (Stainbrook, 1945)

Fig. 6.

*Atrypa desquamata* Sowerby; Sobolev 1909, pp. 221, 367 (partim).

*Atrypa reticularis* L.; Samsonowicz 1917, p. 45.

*Atrypa varicostata* Stainbrook, n. sp.; Stainbrook 1945, pp. 47, 49, pl. 5: 13–17.

*Atryparia* (*Costatrypa*) *varicostata* (Stainbrook); Copper 1973, pl. 2: 9–15.

*Costatrypa varicostata* (Stainbrook); Cooper & Dutro 1982, pp. 88–89; pl. 23: 7–31.

*Costatrypa extensa* sp. n.; Cooper & Dutro 1982, pp. 87–88, pl. 23: 39–56, pl. 24: 1–12.



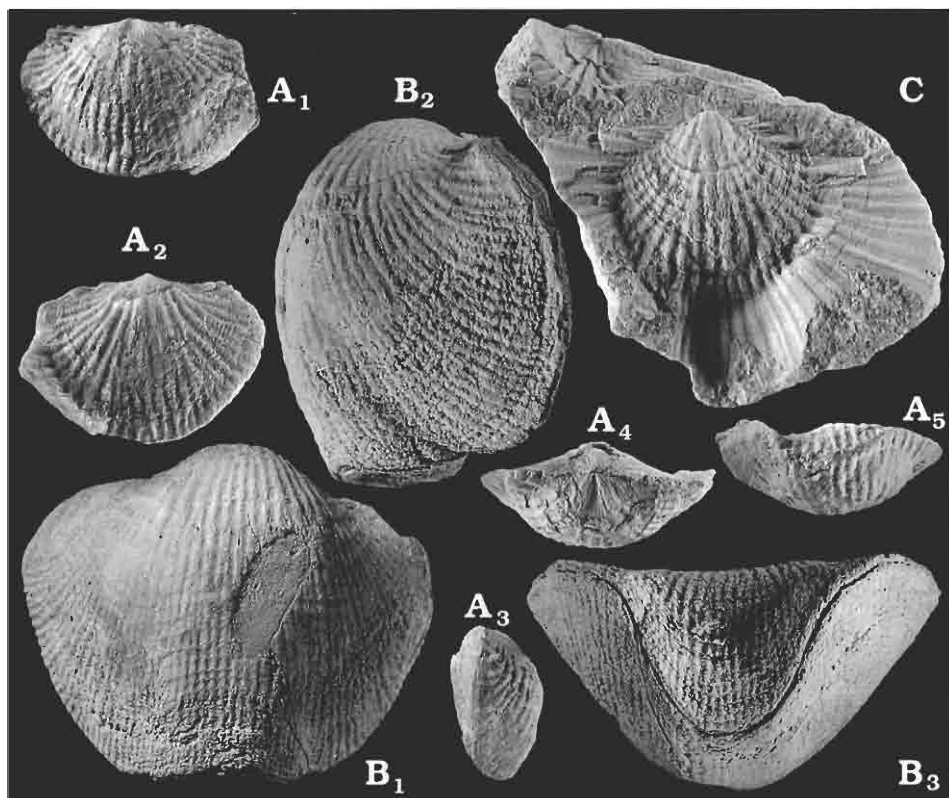


Fig. 6. *Costatrypa varicostata* (Stainbrook, 1945) from Tudorów (A, C) and Kowala road cut (B). A<sub>1</sub>–5. Complete shell GIUS 4-263/14 in dorsal, ventral, lateral, posterior, and anterior views. B<sub>1</sub>–3. Typical morphotype GIUS 4-279/50 in dorsal, lateral, and anterior views. C. Pedicle valve GIUS 4-263/18 with preserved frills. All  $\times 2$ .

**Material.** — Nine complete and seven damaged shells, and 74 fragments of shells and disarticulated valves; some of them are silicified and etched.

**Remarks.** — The specimens from Poland demonstrate two morphotypes. The first, which occurs in the Kowala road cutting and at Łgawa Hill and Kadzielnia, is identical with *Costatrypa varicostata* of Stainbrook (1945), Copper (1973), and Cooper & Dutro (1982). The second morphotype, recovered from probably coeval strata at Tudorów, is almost twice as small as the type and possesses a wider, flattened shell, and a wide, straight hinge line. The second morphotype is identical with *Costatrypa extensa* Cooper & Dutro, 1982 from the Sly Gap Formation of New Mexico, U.S.A. (Cooper & Dutro 1982). According to Day & Copper (1998) *C. extensa* is conspecific with *C. varicostata*, with morphological transitions existing between the two species. In the collection from Poland transition between the two morphotypes does not occur (Fig. 6). We follow the opinion of Day & Copper (1998) because it is based on a numerically very extensive collection.

The Polish specimens (both morphotypes) are similar to *Costatrypa variabilis* Godefroid, 1970 from the middle–late Frasnian of southern Belgium (Godefroid 1970: pp. 98–104, figs 69, pl. 5: 3), but they differ in attaining smaller shell dimensions, and in having thinner radial ornamentation in the anterior part of the shell.

**Occurrence.** — The Late Frasnian Independence Shale of Iowa and Sly Gap Formation of New Mexico, USA (Stainbrook 1945; Cooper & Dutro 1982); the Holy Cross Mountains in Kowala road

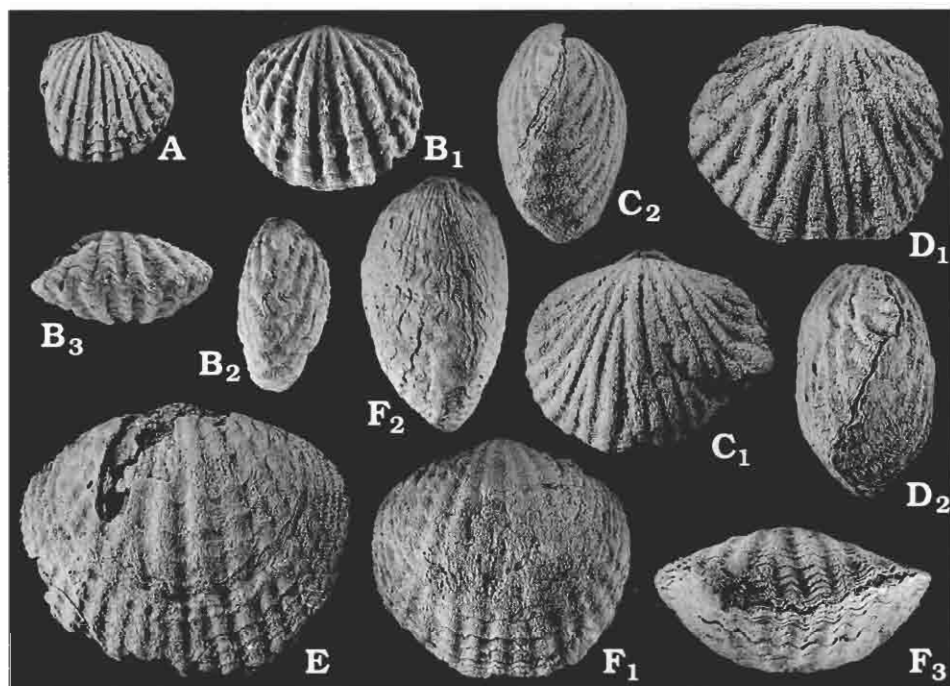


Fig. 7. Late Frasnian Spinatrypinae from Kowala (road cut; A, B, E, F) and Łgawa Hill (C, D). A, B. *Spinatrypa* ex gr. *bifidaeformis* (Chernyshev, 1887), ventral (A, B<sub>1</sub>), lateral (B<sub>2</sub>), and anterior (B<sub>3</sub>) views; GIUS 4-279/5 (A), GIUS 4-279/6 (B). C, D. *Spinatrypa* (?) sp. A, two specimens in dorsal and lateral views; GIUS 4-284/301 (C), GIUS 4-284/303 (D). E, F. *Spinatrypa* ex gr. *semilukiana* Lyashenko, 1959, in ventral (E), dorsal (F<sub>1</sub>), lateral (F<sub>2</sub>), and anterior (F<sub>3</sub>) views; GIUS 4-284/3 (E), GIUS 4-284/1 (F). All  $\times 2$  except B  $\times 5$ .

cutting and quarry (set H-1 to H-2) and Łgawa Hill (set R), *P. rhenana* Zone (maybe also *P. linguiformis* Zone); the Detrital Limestones to Platy(?) Limestones Units at Tudorów, eastern part of the Holy Cross Mountains, Poland, later Frasnian (?*P. jamieae*–*P. rhenana* zonal interval; Godefroid & Racki 1990); one loose specimen has also been found at Kadzielnia (?from set C, *Manticoceras* Limestone).

## Subfamily Spinatrypinae Copper, 1978

### Genus *Spinatrypa* Stainbrook, 1951

#### *Spinatrypa* ex gr. *bifidaeformis* (Chernyshev, 1887)

Fig. 7A, B.

**Material.** — Two complete to nearly complete shells, and three fragments of shells, all silicified.

**Remarks.** — The minute specimens from Kowala (L less than 10 mm) mostly exhibit mature features and are related to the early Frasnian *S. bifidaeformis* (Chernyshev, 1887) *sensu stricto* (Nalivkin 1941: p. 171, pl. 5:9), but not in the broad sense of Nalivkin (1947; see below). The ventral beak is larger and more acute in the Holy Cross specimens, but a tendency to stronger development of the ventral median (carina-like) ribs, and the single median dorsal rib, is well expressed. A similar rib pattern also occurs in the larger-sized early Frasnian spinatrypinids from the Kadzielnia Member (Kadzielnia, set A; Kowala, set C; Łgawa Hill–Jazwica, set J), determined as *Spinatrypa plicata* Rzhonsnitskaya, 1964 by Biernat (1971: p. 147, pl. 4: 1–6, pl. 8: 4).

The diminutive *Spinatrypa* (*Plicspinatrypa*) *plicata* (Rzhonsnitskaya, 1964) from the latest Frasnian of Kuzbass (Rzhonsnitskaya 1964: p. 108, pl. 1: 13; Rzhonsnitskaya 1975: p. 124, pl. 25: 15, fig. 37; Rzhonsnitskaya *et al.*, 1998) shows a comparable shell and beak, but the ribs are coarser (only 7–8) and simple.

**Occurrence.** — Holy Cross Mountains, Kowala road cutting (units II–III, Miklas in Racki *et al.* 1993), late Frasnian (Late *P. rhenana* Zone only?).

### *Spinatrypa* ex gr. *semilukiana* Lyashenko, 1959

Fig. 7E, F.

*Spinatrypa*; Miklas in Racki *et al.* 1993, pl. 6: 3.

**Material.** — Three complete and three damaged shells, and more than 10 fragments of shells and valves, all silicified and from Kowala.

**Remarks.** — A medium-sized (L up to 20 mm) species with up to 14 strong and mostly bifurcating ribs, which is related to the stratigraphically older Frasnian *S. semilukiana* species group from the East European Platform (Lyashenko 1959: p. 158, pl. 38: 1–5; p. 174, pl. 51: 1, 2), and from Dębnik (Baliński 1979: p. 60, pl. 13: 5, 7–10, pl. 14: 6; see also Racki 1993a: fig. 11J, K). As summarized by Baliński (1979: p. 60), the underdevelopment of a median groove on the brachial valve and a distinctly raised mid-rib pair on the pedicle valve are important diagnostic features for *S. semilukiana*, differentiating it from the related species *Spinatrypa bifidaeformis* (Chernyshev, 1887) (Sarytcheva & Sokolskaya 1952: p. 173; Lyashenko 1959: p. 174). This character is only incipiently developed on the shells under study, being limited to the posteriormost portion of the shell. However, the principal difference lies in the small pedicle beak and narrow interareas, as well as in the slightly finer ribbing (4–6 per 10 mm near the anterior margin in typical specimens).

**Occurrence.** — Holy Cross Mountains, Kowala road cutting (set H, units II–III, Miklas in Racki *et al.* 1993), late Frasnian (Late *P. rhenana* Zone only?).

### Genus *Spinatrypina* Rzhonsnitskaya, 1964

#### Subgenus *Exatrypa* Copper, 1967

#### *Spinatrypina* (*Exatrypa*) aff. *kuniandia* Grey, 1978

Fig. 8C, D.

*Atrypa aspera* Schlotheim; Sobolev 1909, pp. 188, 367 (*partim*).

aff. *Spinatrypina* (*Exatrypa*) *kuniandia*. sp. n.; Grey 1978, p. 45: pl. 5: 1–3.

**Material.** — Ten complete to nearly complete shells, and more than 40 fragments of shells and valves, partly exfoliated and embedded in rock.

**Remarks.** — Shells that are mostly transversely elliptical shells are included in the subgenus *S. (Exatrypa)*, even if extreme variants are almost circular in outline. *S. (E.)* aff. *kuniandia* is comparable with some specimens of *S. (E.) explanata* (Schlotheim, 1820), illustrated as a variety on pl. 20: 3, 4 by Copper (1967). Nevertheless, more resemblance is noted to the Australian species *S. (E.) kuniandia* Grey, 1978 from the Frasnian reef complex (Pillara and Sadler Formations), manifested in a similar shell shape and tubular-imbricate ribbing. The Polish spinatrypinids are generally less transversally elongated, smaller in size ( $W = 17$  mm in comparison to 24 mm for the type specimens), as well as devoid of a frilly extension along the edges of growth lines, but the last is possibly due to exfoliation of the shell.

**Occurrence.** — Holy Cross Mountains, (Grabina, set B); later Frasnian (?Late *P. hassi* to Early *P. rhenana* Zones).

#### *Spinatrypina* (*Exatrypa*) *relicta* sp. n.

Figs 9, 10A–G, 11, 12A and 13K.

Holotype: Complete shell IGUS 4-284/16; Fig. 9.

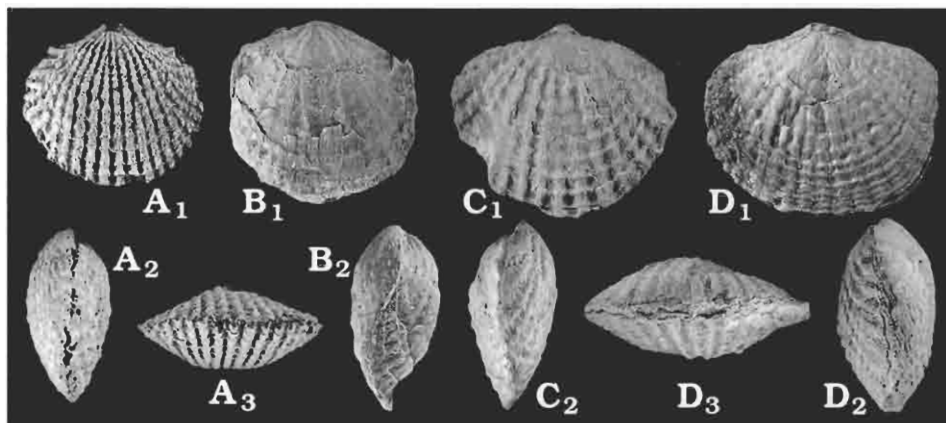


Fig. 8. Late Frasnian *Spinatrypina* from Łgawa Hill (A), Kadzielnia (B), and Grabina (C, D). A, B. *Spinatrypina* (*Spinatrypina*) sp., dorsal (A<sub>1</sub>, B<sub>1</sub>), lateral (A<sub>2</sub>, B<sub>2</sub>) and anterior (A<sub>3</sub>) views of differently sized and preserved specimens GIUS 4-284/211 (A) and GIUS 4-271/1 (B). C, D. *Spinatrypina* (*Exatrypa*) aff. *kuniandia* Grey, 1978, shells GIUS 4-277/51 (C) and GIUS 4-277/53 (D) in dorsal (C<sub>1</sub>, D<sub>1</sub>), lateral (C<sub>2</sub>, D<sub>2</sub>), and anterior (D<sub>3</sub>) views. All  $\times 2$ .

Type locality: Łgawa Hill (= eastern Jaźwica Quarry) near Bolechowice, Holy Cross Mountains, Poland.

Type horizon: Thin-bedded nodular-marly set (complex R; Racki 1981, 1993b); late Frasnian, *P. rhenana* conodont Zone.

Derivation of the name: *relicta* – occurring during the latest phase of the atrypid evolution.

**Diagnosis.** — *S. (Exatrypa) relicta* is half the size of the middle Frasnian *S. (E.) planata* (Biernat 1971: p. 149, pl. 4: 9–11, pl. 8: 2, 3; fig. 7), and is also a less transverse, convexoplane rather than dorsi-biconvex shell, with variable but relatively strong subtubular ribbing. It differs from the similarly sized *S. (Exatrypa)* aff. *kuniandia* Grey, 1978 in the distinctive subtubular ribs (without imbricated appearance), and in a transversely elongated and flattened shell shape.

**Material.** — Thirty two complete to nearly complete shells, and more than 20 fragmentary shells and valves, all silicified and sometimes etched.

Dimensions (in mm):

Cat. No. IGUS 4-284	Lvv	Ldv	W	T	R-5
170 (holotype)	13.6	13.0	16.1	7.8	4
171	9.1	8.5	10.9	4.1	4–5
173	14.0	13.4	20.0	6.9	5
176	12.0	11.3	(14.5)	6.0	4

**Description.** — Shells small-sized for the subgenus (W less than 20 mm), convexoplane to moderately dorsi-biconvex, semi-oval to strongly transversely elongated, flattened; cardinal margin nearly straight, anterior commissure uniplicate. Pedicle valve beak prominent, erect to slightly incurved, with relatively large orthocline to anacline interareas; apical foramen flanked by two small deltidial plates.

Moderately thin tubular ribs, eight to ten per 10 mm near the anterior margin, increasing variously by bifurcation and intercalation, and expanding distally; ventral median keel formed by mid-rib pair; dorsal median groove more or less developed. Growth lamellae present only

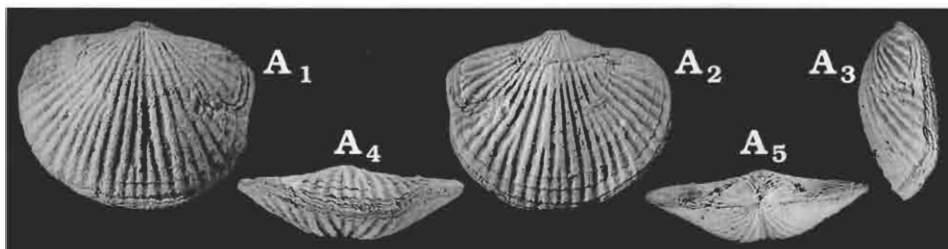


Fig. 9. *Spinatrypina (Exatrypa) relict* sp. n. from the late Frasnian of Łgawa Hill; A<sub>1</sub>–5. Holotype (morphotype B) GIUS 4-284/170 in dorsal, ventral, lateral, anterior, and posterior views. All  $\times 2$ .

anteriorly (two to four per 5 mm), adhering to the shell and crowded toward the margin; microlines dense (two to four per mm).

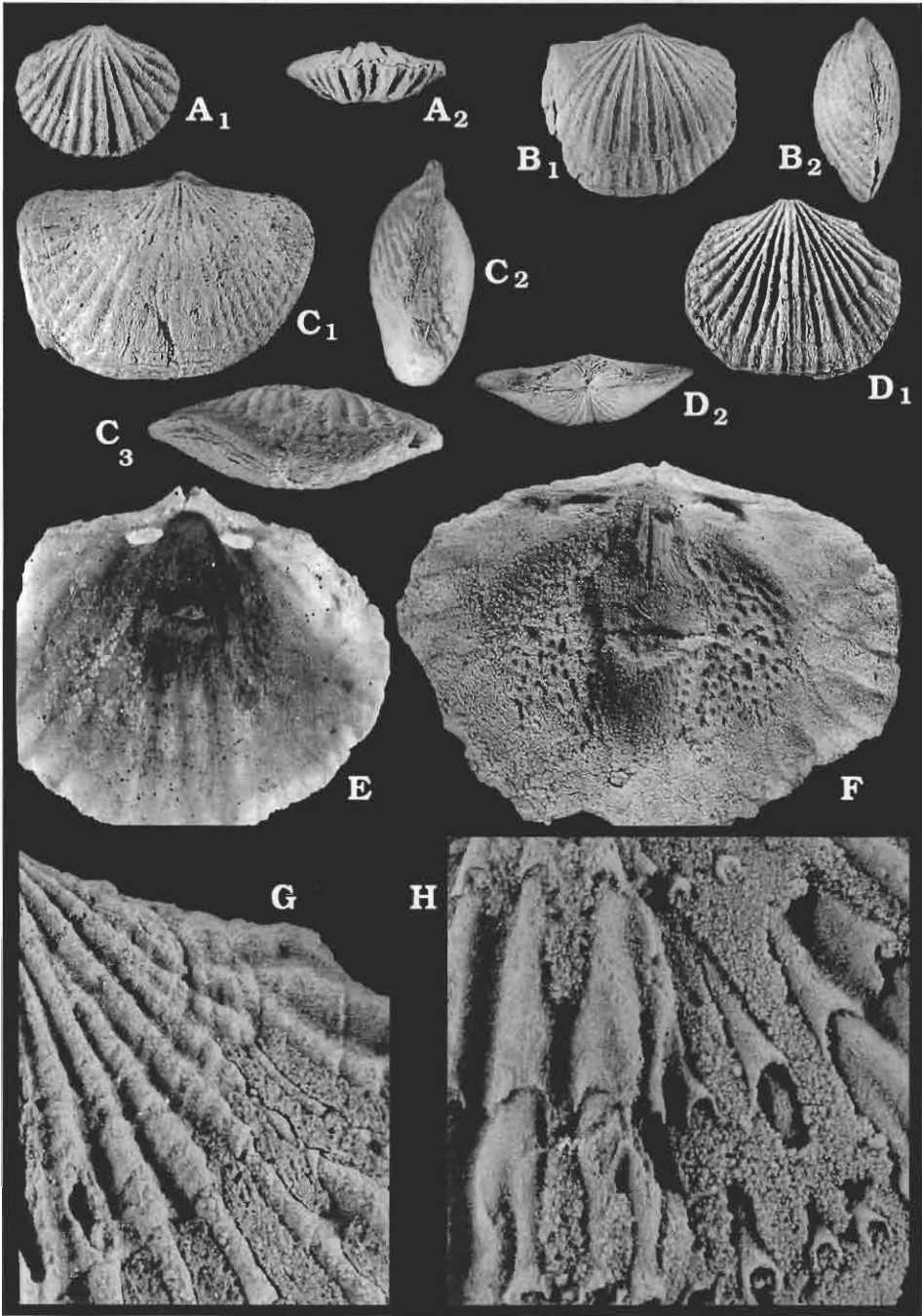
The shell is relatively thick-walled. Interior of pedicle valve with solid, distinctly crenulated teeth, pointed nearly vertically or slightly inwardly; dental cavities apparently absent (Fig. 10E); thick-shelled specimens with impressed muscle scars, elevated anteriorly; gonadal pits distinct. In brachial valve, hinge plates quite massive, sockets deep, strongly crenulated on dorsal surface, supported by short and broad median ridge (Fig. 10F).

**Variability.** — Ribbing is the most variable character, and the more coarsely ornamented morphotype B (Fig. 10A–C) is distinguishable from the more common, finely costate forms, treated as morphotype A (Figs 9, 10D). Among other external features, the shell shape variation comprises a noticeable transition from more shield-shaped, inflated specimens to transverse, flattened varieties (see Fig. 12A).

**Remarks.** — The new species proposed herein is probably an end-member in the evolutionary lineage (see Copper 1967: p. 123, fig. 17), derived from a variety of *S. (E.) explanata* (Schlotheim, 1820) exemplified by the lectotype (Copper 1967: pl. 20: 1, 2), and originated within the Laurussian shelf. Copper (1967) noted a distinct tendency toward flat shape, greater size and weakly imbricate, more strong tubular ribbing as marked features determining the transition from more globose *S. (Spinatrypina)* to *S. (Exatrypa)*, probably near the Middle–Upper Devonian transition (see Fig. 11). This evolutionary trend continued in the early Frasnian, as seen in the transition from *S. (E.) tubaecostata* (Paeckelmann, 1913) to *S. (E.) explanata*, culminating in the mid-Frasnian, when the *S. (E.) planata*–*S. (E.) relict* species group originated. The carinate pedicle valve, a character especially clearly seen in some specimens of *S. (E.) relict*, is usually rare in *Spinatrypina*, but common in *Spinatrypa* (see e.g., Fenton & Fenton 1924; Stainbrook 1945; see above). The weak spinosity exhibited by *S. (E.) planata* from Kadzielnia (see Fig. 10M) is also atypical for *Spinatrypina*. Gürich (1896: p. 272) noted the resemblance of the Kadzielnia species to the prominently carinate species *Carinatina plana* (Kayser, 1871), and external analogies with the unusual Middle Devonian carinate genera *Eifelatrypa* Copper, 1973 and *Carinatrypa* Copper, 1973 are indeed remarkable. *S. (S.) relict* sp. n. can be compared only with an aberrant species of *S. (Exatrypa)* from the early Frasnian of British Columbia (Copper 1978: p. 301), cited by Maurin & Raasch (1972: p. 65, pl. 5: 10–20) as an undescribed genus recalling the orthoid *Tropidoleptus*.

The second lineage of the Frasnian spinatrypinids can be derived from the smaller and more rounded variety of *S. (E.) explanata* (Copper 1967: pl. 20: 3, 4). It is represented in the later Frasnian

Fig. 10. *Spinatrypina (Exatrypa)* from the Frasnian of Łgawa Hill (A–G) and Kadzielnia (H). A–G. *Spinatrypina (Exatrypa) relict* sp. n., dorsal (A<sub>1</sub>, B<sub>1</sub>, C<sub>1</sub>), ventral (D<sub>1</sub>), lateral (B<sub>2</sub>, C<sub>2</sub>), anterior (A<sub>2</sub>, C<sub>3</sub>), and posterior (D<sub>2</sub>) views of differently-ribbed specimens. A, B. Morphotype B, GIUS 4-284/171 (A) and GIUS 4-284/172 (B). C, D. Morphotype A; GIUS 4-284/173 (C) and GIUS 4-284/175 (D). E, F. Internal



view of two ventral valves GIUS 4-284/181 and GIUS 4-284/182, note well visible dorsal muscle and vascular scars. G. Details of ornamentation. H. *Spinatrypa* (*Exatrypa*) *planata* Biernat, 1971, details of ornamentation, note a weak spinosity, GIUS 4-270/21. All  $\times 2$  except E, F  $\times 5$  and G, H  $\times 10$ .

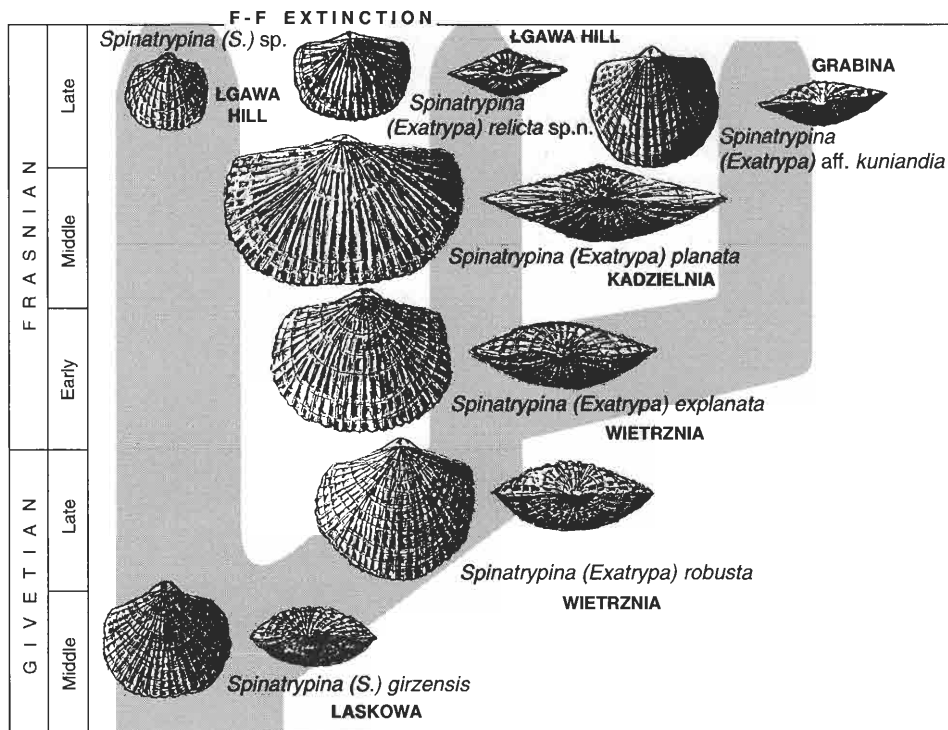


Fig. 11. Evolutionary chart of Spinatrypinae during middle Givetian to late Frasnian, based on faunas from the Holy Cross Mountains (see also Copper 1967: fig. 17).

by the here described *S. (Exatrypa) aff. kuniandia* and *S. (E.)* sp. B of Godefroid & Helsen (1998: fig. 4G–K).

The spinatrypinid data from the Holy Cross Mountains point either to misinterpretation of the species sequence within *S. (Exatrypa)* in the Renish Frasnian, as reconstructed by Copper (1967) from isolated localities, or to reversed evolutionary transition back towards more globose forms in this part of the Laurussian shelf. The atrypid data from the Ardennes (Godefroid & Jacobs 1986) support the former possibility.

**Occurrence.** — Holy Cross Mountains, Łgawa Hill (Jaźwica) Quarry (set R), Kowala Quarry (set H-1), late Frasnian (*P. rhenana* Zone).

### *Spinatrypa*(?) sp. A

Fig. 7C, D.

**Material.** — Two complete and three damaged shells, and five fragments of shells and valves, strongly silicified.

**Remarks.** — The small-sized (W less than 18 mm), ovate, moderately dorsibiconvex carinate shells are quite different from typical spinatrypinids due to the scarcity of concentric growth lamellae; however, a merely preservational effect cannot be excluded in these silicified shells. Coarse and simple ribs (in smaller forms) resemble those of *Spinatrypa (Plicspinatrypa) plicata* (Rzhonsnitskaya, 1964), whilst the strong biconvexity and irregularly bifurcating ribs suggest affinity with '*Anatrypa*' *heckeri* Nalivkin, 1941.

**Occurrence.** — Holy Cross Mountains, Łgawa Hill (Jaźwica) Quarry (set R), Kowala Quarry (set H-1), late Frasnian (*P. rhenana* Zone, ?also in the *P. linguiformis* Zone).

## Other spinatrypinids

Fig. 8A, B.

**Remarks.** — Mostly minute (but occasionally attaining 20 mm in W), roundish to slightly transversely outlined, dorsibiconvex and variably uniplicate spinatrypinids (*Spinatrypina* and *Spinatrypa*) are known from Kadzielnia (*Manticoceras* Limestone and older units; see Biernat 1971) and other middle to late Frasnian localities (e.g., Psie Górki; see Gawlik in Racki *et al.* 1993: pl. 12: 7). They seem to represent mostly the '*Spinatrypa tubaecostata*' group common in the Frasnian of the East European Platform, as shown by Nalivkin (1947) and Lyashenko (1959). However, after revision by Copper (1967), *Atrypa tubaecostata* Paeckelmann, 1913 is restricted to the more transversely elongated, flattened forms of the subgenus *S.* (*Exatrypa*) from the Rhenish Givetian to Frasnian passage beds (see Fig. 11). The poorly preserved material does not demonstrate the surface sculpture adequately (see also similar spinatrypinids in Baliński 1979: p. 59 and Racki 1993a: p. 312).

## Subfamily Pseudogruenewaldtiinae Rzhonsnitskaya, Yudina & Sokiran, 1997

### Genus *Iowatrypa* Copper, 1973

#### *Iowatrypa americana* (Stainbrook, 1945)

Figs 12B, 13B–H, J, L.

*Gruenewaldtia americana* sp. n.; Stainbrook 1945, p. 52, pl. 5: 18–23, 27, 28; fig. 1 (6); Day & Copper 1998: p. xx., figs xxx..

*Iowatrypa americana* (Stainbrook); Copper 1973, pl. 2: 1–4; Cooper & Dutro 1982: pl. 24: 13, 14. ?*Iowatrypa*; Gawlik in Racki *et al.* 1993, pl. 12:5.

?*Iowatrypa markowskii* (Lyashenko); Baliński 1979, pp. 57–58, pl. 14: 1–5; fig. 20.

**Material.** — Forty two complete or nearly complete shells, and more than 30 fragments of shells and valves, all silicified and sometimes etched; three damaged shells and over 30 valves embedded in limestone, chiefly exfoliated.

**Remarks.** — Godefroid (1994: pp. 90–91) reviewed the interspecific distinction within this genus, with emphasis on overall shell form, and sinus and fold development. However, the intraspecific variability of most species of *Iowatrypa* is unknown. The material under study from Łgawa Hill displays a wide variability of diagnostic features, including pedicle umbo and interarea. Many specimens show close relationships with the late Frasnian species *Iowatrypa americana* (Stainbrook, 1945).

Similar data on intraspecific variability were presented by Baliński (1979) for the Dębnik species, included in *I. markowskii* (Lyashenko, 1959). However, diagnostic characters for the early Frasnian Russian species, such as a 'square' shell outline and a median groove on the brachial valve (see Lyashenko 1973: p. 80, pl. 21: 1–8), are rarely observed in the Holy Cross specimens. *Iowatrypa* species from the Holy Cross Mountains and Dębnik are quite similar, however, and the latter may also belong to *I. americana*. One difference lies in the slightly finer ribbing of the Polish specimens.

**Occurrence.** — Holy Cross Mountains, Łgawa Hill (Jaźwica) Quarry (set R), Kowala Quarry (set H-1), questionably Psie Górki (set G), Wietrzna (set F), and Sobiekurów; late Frasnian (*P. rhenana* Zone up to the latest *P. linguiformis* Zone); probably also the Grained Limestone, late Frasnian (*P. rhenana* Zone) at Dębnik anticline, southern Poland (Baliński 1979, 1995); late Frasnian Owen Mbr., Cerro Gordo Fm. and perhaps Independence Shale of Iowa, U.S.A. (see discussion in Day 1998).

## Genus *Waiotrypa* Baliński, 1997

### *Waiotrypa sulcicarina* Baliński, 1997

Fig. 13A, I.

**Material.** — Thirty complete and 19 damaged shells, and 21 fragments.



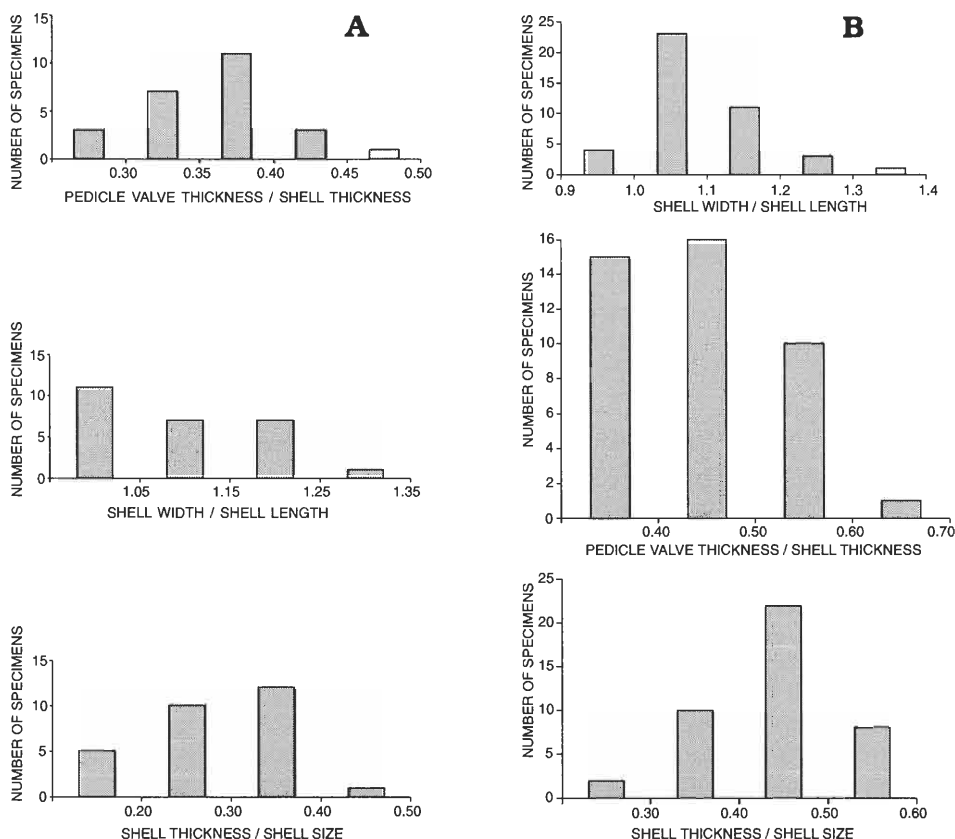


Fig. 12. Frequency diagrams for principal shell indexes for *Spinatrypina (Exatrypa) relicta* sp. n. (A) and *Iowatrypa owenensis* (Webster, 1921) (B), to show range of intraspecific variability.

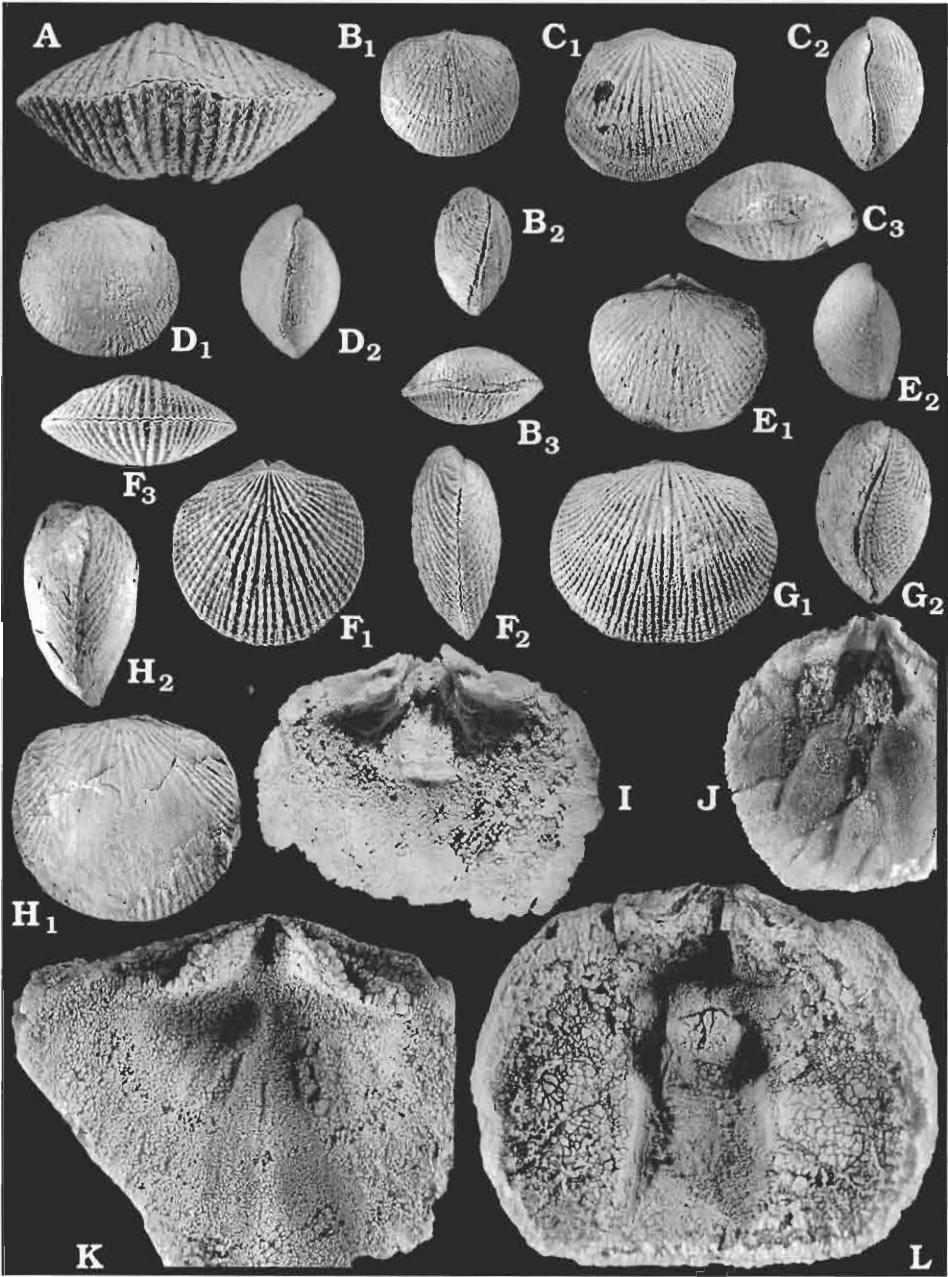
**Remarks.** — The subfamily affiliation of *Waiotrypa* is somewhat uncertain. The genus shares many external features with the pseudogruenewaldtiinid *Iowatrypa* Copper, 1973 (Baliński 1997). It is very difficult to separate the members of these two genera when they co-occur in the same sample. On the other hand, the presence of high, distinct ventral areas and small dental nuclei suggest attribution of *Waiotrypa* to Spinatrypinae, as suggested by Copper (written communication). The ventral muscle platform of *Waiotrypa* is incised posteriorly, but raised anteriorly as in *Iowatrypa* (Fig. 13I, compare with Godefroid 1994: fig. 5).

**Occurrence.** — Holy Cross Mountains, Łgawa Hill (complex R), Kowala road cutting (middle part?); late Frasnian (*P. rhenana* Zone).

## Other pseudogruenewaldtiinids

Fig. 13H.

Fig. 13. Late Frasnian Pseudogruenewaldtiinae (A–I, J–L) and Spinatrypinae (K) from Łgawa Hill (A–F, K, L), Miedzianka (H), and Kowala quarry (J). A, I. *Waiotrypa sulcicarina* Baliński, 1997, anterior view of holotype GIUS 284/117 showing sulcate brachial and carinate pedicle valves (A); internal view of pedicle valve, GIUS 284/80 (I). B–G, J, L. *Iowatrypa americana* (Stainbrook, 1945), dorsal (B1–G1), lateral (B2–G2),



and anterior (B<sub>3</sub>, C<sub>3</sub>, F<sub>3</sub>) views of six specimens to show broad intraspecific variability in shell outline, size, and interarea development; GIUS 4-284/200 (B), GIUS 4-284/201 (C), GIUS 4-284/202 (D), GIUS 4-284/203 (E), GIUS 4-284/205 (F), and GIUS 4-284/204 (G). J, L. Internal view of two pedicle valves, GIUS 4-284/225 (L) and GIUS 4-285/22 (J) to show thickened shell and raised muscle scars. H. *Iowatrypa* sp., in dorsal and lateral views, GIUS 4-299/1. K. *Spinatrypa* (*Exatrypa*) *relicta* sp. n., internal view of brachial valve GIUS 4-284/183. All × 2 except J–L × 5.

**Remarks.** — Medium-sized biconvex shells, with occasionally preserved imbricate-tubular ribbing, were collected from the late Frasnian reef-type limestones at Miedzianka (Fig. 13H, I). The specimens increased the observed extent of variation within *Iowatrypa*, but poor preservation preclude such a comparison with *I. americana*.

In addition, a single markedly ventri-biconvex, ovoid shell (L = 33 mm) has been found loose at Kadzielnia. Similar but more subquadrate atrypids, represented by rare, strongly convex pedicle valves only, occur at Łgawa Hill (set R). The fine ribbing is of the tubular type (R-5 up to 8), resembling more that of the coeval species *Desquamatia* (D.) *alticoliformis* than true *Pseudogruenewaldtia* (see Rzhonsnitskaya *et al.* 1998). Alekseeva (in Alekseeva *et al.* 1996) proposed as new species *P. elongata* from Yakutia with probably similarly weakly developed growth lamellae.

## Subfamily Variatrypinae Copper, 1973

### Genus *Desquamatia* Alekseeva, 1960

#### Subgenus *Desquamatia* (*Desquamatia*) Alekseeva, 1960

#### *Desquamatia* (*Desquamatia*) *alticoliformis* Rzhonsnitskaya, 1975

Fig. 14.

*Atrypa desquamata* Sowerby; Gürich 1896, p. 271 (*partim*); Sobolev 1909, p. 367 (*partim*).

*Desquamatia* (*Desquamatia*) *alticoliformis* sp. n.; Rzhonsnitskaya 1975, p. 131, pl. 28: 10–13; fig. 41.

*Desquamatia* (*Desquamatia*) *alticoliformis* Rzhonsnitskaya, 1975; Godefroid & Helsen 1998, pp. 16–17, figs 10B, 11A–G, 12; Rzhonsnitskaya *et al.* 1998, p. xx, figs xx.

**Material.** — Thirty three complete or nearly complete shells, 34 damaged shells, and 15 fragments of isolated and silicified valves frequently preserving details of internal structure.

**Remarks.** — The generic assignment of the species is controversial and, moreover, it has an important consequence as it extends this otherwise Middle Devonian genus (Copper 1998) into the late Frasnian. The Polish form seems to be conspecific with the Russian species and both demonstrate very fine radial ornamentation and rare and weak concentric growth lamellae. We agree with the opinion of Godefroid (1998: p. 17) and Copper (written communication) that the species should be better placed within the genus *Desquamatia*.

*D. (D.) alticoliformis* occurs abundantly in complex R at Łgawa Hill, which can be correlated with the *P. rhenana* conodont Zone. Similar specimens, most probably the same species, come from slightly older strata at Grabina. Some of those specimens appear to have slightly coarser ribbing ornamentation in comparison to specimens from Łgawa Hill.

**Occurrence.** — Bedded-nodular marly limestones at the Łgawa Hill (complex R) and Kowala sites (set H-2); several fragmentary specimens from the detrital limestones that crop out in the Grabina quarry (upper part of set B); the species probably occurs in some other sites in similar lithologies (e.g. Kadzielnia, sets B, C; *P. hassi* to Late *P. rhenana* Zone). Late Frasnian of Kuznetsk Basin, Urals, South Timan, Novosibirsk area, and Western Fergana, Russia (Rzhonsnitskaya *et al.* 1998) and Ardennes (Godefroid & Helsen 1998).

## Genus *Radiatrypa* Copper, 1978

### *Radiatrypa* aff. *alticola* (Frech, 1891)

Fig. 15.

*Anatrypa alticola* (Frech); Baliński 1979, pp. 52–53, pl. 10: 1–3.

**Material.** — One complete shell, one slightly damaged shell and two fragments of pedicle valves.

**Remarks.** — This is an uncommon species in the collection from Łgawa Hill. It can be recognized by its rounded outline, its near biconvexity, its high pedicle valve interareas and by very fine radial ornamentation. This species seems to be related to *Atrypa desquamata* var. *alticola* Frech (1891: p. 680, pl. 44: 1) from the Givetian of the Carnic Alps, as it has the same type of shell shape and shell ornamentation. Externally almost identical forms assigned to *Atrypa alticola* are described from several Frasnian localities in Russia (Nalivkin 1930: pp. 99–100, pl. 7: 2, 5; 1947: p. 100, pl. 22:

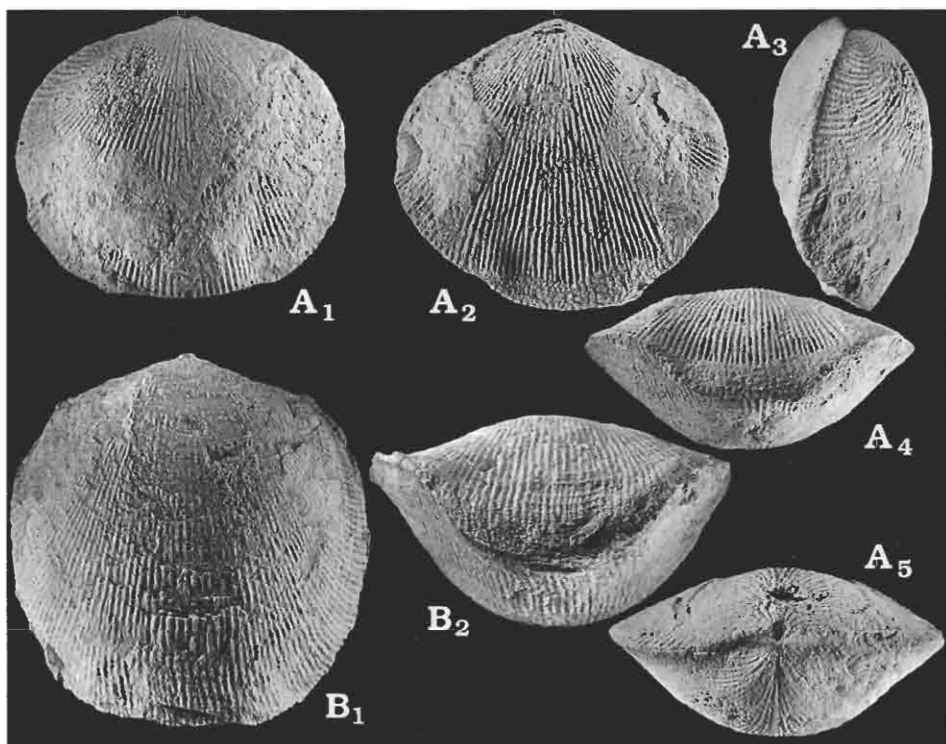


Fig. 14. *Desquamatia (Desquamatia) alticoliformis* Rzhonsnitskaya, 1975 from Łgawa Hill. A<sub>1</sub>-5. Complete shell GIUS-4-284/134 in dorsal, ventral, lateral, posterior, and anterior views. B<sub>1</sub>-2. Large shell GIUS-4-277/210 in dorsal and anterior views. All  $\times 2$ .

14, 15; 1951: p. 17, pl. 4: 1; Adrianova 1955: p. 368, pl. 7: 1; Mikriukov 1955: pp. 240-241, pl. 5: 4). The specimens from Łgawa Hill are identical externally with those of *Anatrypa alticola* from the Late Frasnian of the Dębnik anticline (southern Poland) (Baliński 1979: pp. 52-53, pl. 10: 1-3). As was noted earlier (Baliński 1979: p. 53) the Frasnian specimens referred to Frech's species are morphologically very similar to the type specimens, which come from the Givetian. Most probably the Frasnian collections represent another species closely related to *Radiatrypa alticola*.

The specimens from Poland are also very similar to the early Frasnian *R. tenuisulcata* (Venjukoff, 1886) from the Pskov Beds of the East European Platform (Nalivkin 1941: pp. 167-168, pl. 5: 10, 11, pl. 8: 7; Copper 1978: p. 293, pl. 5: 6-10). However, the Russian form, which is rare and poorly known, seems to be more finely ribbed.

**Occurrence.** — The late Frasnian complex R of Racki (1981) at Łgawa Hill (*P. rhenana* Zone), Holy Cross Mountains; the Grained Limestone (*P. rhenana* Zone) in the Dębnik anticline, southern Poland (Baliński 1979, 1995).

## Other variatrypinids

Fig. 16.

**Remarks.** — Numerous medium-sized atrypids from the 'reefal' facies (primarily at Grabina and Kadzielnia; Fig. 16A, B) display circular to transversely suboval (to shield-shaped), dorsibiconvex to subequally biconvex shells, with uniplicate anterior commissure. The ventral beak is slightly curved, but the interareas are rarely exposed. The mostly fine ribs (R-5 up to 7-8) are tubular-in-

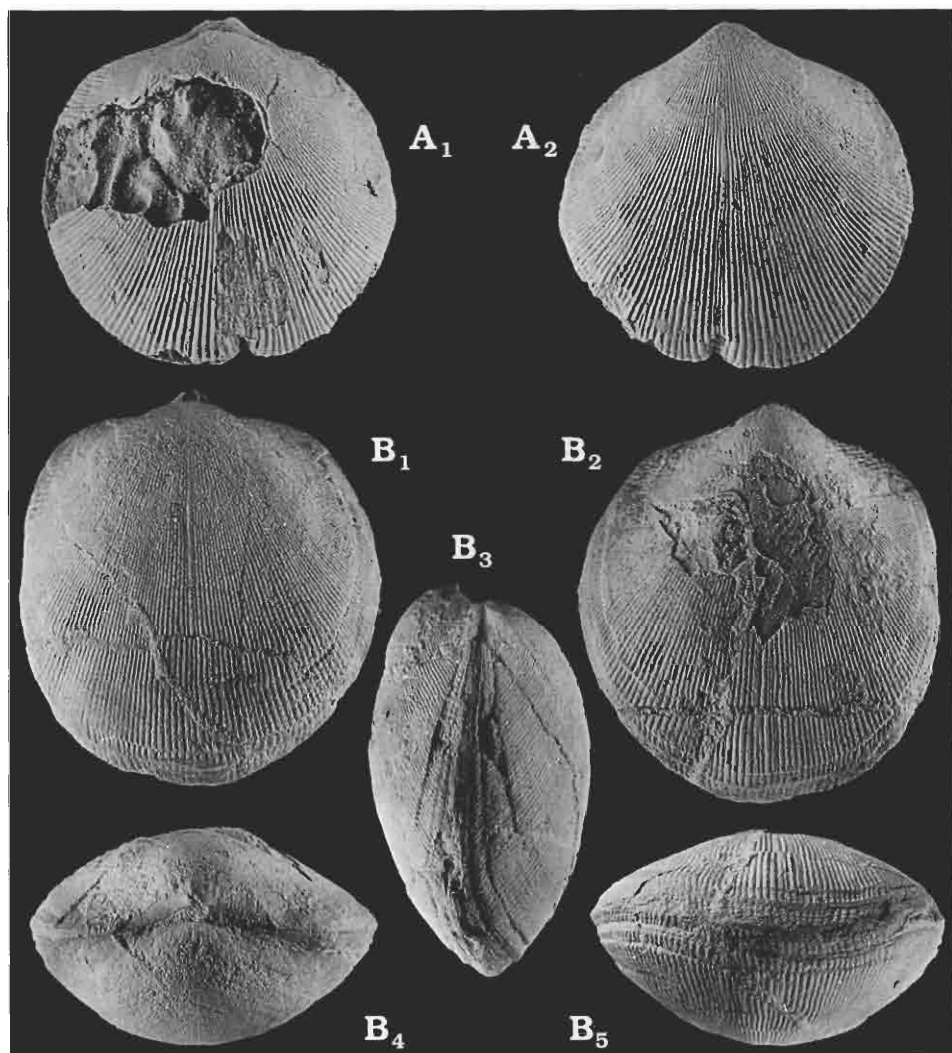


Fig. 15. *Radiatrypa* aff. *alticola* (Frech, 1891) from Łgawa Hill. **A**<sub>1-2</sub>. Slightly damaged shell GIUS 4-284/136 in dorsal and ventral view. **B**<sub>1-5</sub>. Complete shell GIUS 4-284/135 in dorsal, ventral, lateral, posterior, and anterior views. All  $\times 2$ .

terrupted to weakly sublamellar in structure, occasionally with frills. The state of preservation precludes more detailed subdivision of the species group, although it probably includes representatives of the subgenera of *Desquamatia*, as well as relatives of *D. (D.) alticoliformis* (see above) and earlier Frasnian Variatrypinae from the Kadzielnia Limestone Member (see Biernat 1971; Racki 1993a). For example, several specimens from Kadzielnia (set B) are similar to *D. (D.?) schroeteri* Copper, 1967 (pp. 130–131, pl. 26: 3, pl. 27: 2, 3) from the early Frasnian of the Rheinische Schiefergebirge. *Atrypa kadzielniae* Gürich, 1896, described briefly (but not figured) from Kadzielnia (Gürich 1896, 1901), represents a variatrypid species (Racki 1993a: p. 308). Co-occurring and difficult to separate, albeit better preserved, *Variatrypa* and *Desquamatia* are also described from late Frasnian rocks of the Ardennes (Godefroid & Helsen 1998).

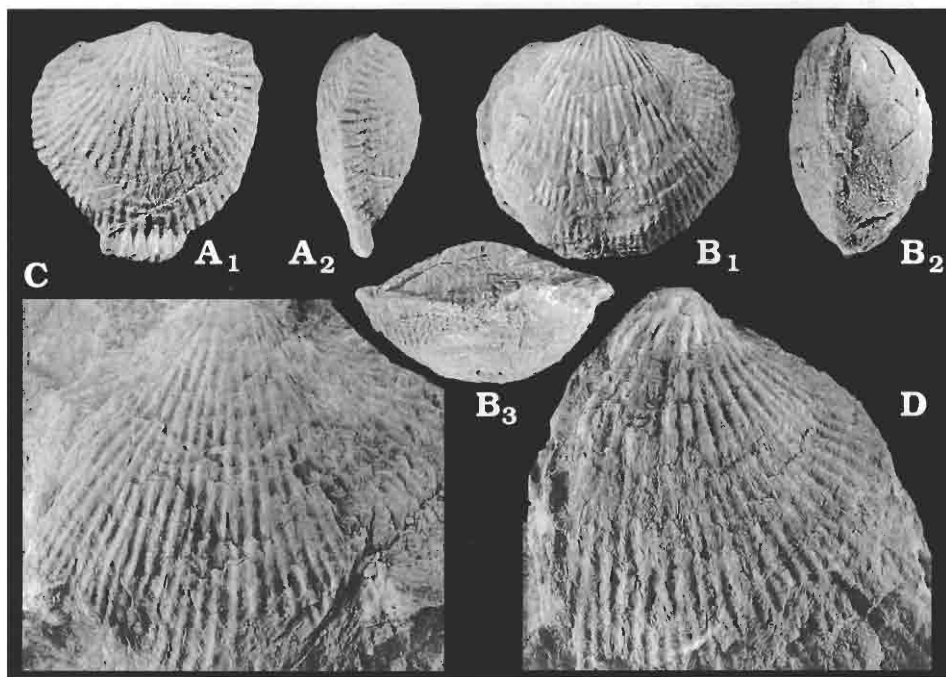


Fig. 16. Late Frasnian Variatrypinae from Grabina (A, B), Psie Górki (C) and Kowala quarry (D); ventral (A<sub>1</sub>, B<sub>1</sub>, C, D), lateral (A<sub>2</sub>, B<sub>2</sub>), and anterior (B<sub>3</sub>) views of four differently-sized specimens; shells GIUS 4-277/201 (A) and GIUS 4-277/200 (B); ventral valves GIUS 4-273/11 (C) and GIUS 4-303/1 (D), note preserved frills (A). All  $\times 2$  (A, B) and natural size (C, D).

In addition, large-sized (W up to 40 mm) and coarsely-ribbed (R-5 between four and six) problematic Variatrypinae, but known from isolated valves only (Fig. 16C, D), are found in the Kowala Quarry (set G) and Psie Górki (unit H-1a), being the stratigraphically youngest atrypid in the latter section.

## Atrypid record of the Kellwasser Crisis in the Holy Cross Mountains

The atrypid-dominated reef-related brachiopod faunas were assigned to the Atrypid-Gypidulid Biofacies by Racki *et al.* (1993), an important shelly community of the Siluro-Devonian stromatoporoid-reef ecosystem (see Figs 17, 19). In the Holy Cross Mountains, diverse atrypids (with *Desquamatia*, *Spinatrypina* in the main roles) are richly represented in the late Givetian to early Frasnian carbonate bank-to-reef succession (see Racki & Baliński 1981; Racki 1993a). A similar association is known from the earliest middle Frasnian Kadzielnia-type stromatoporoid-microbial bioherms (see Biernat 1971; Szulczewski & Racki 1981), as well as in a variety of peri-reefal settings, especially in parautochthonous pockets near *Renalcis*-dominated 'reefs' of the late, but not latest Frasnian (Racki *et al.* 1993). The taxonomic composition of the associations remained similar, and a main innovation of the 'reef-cap' phase during the IId T-R

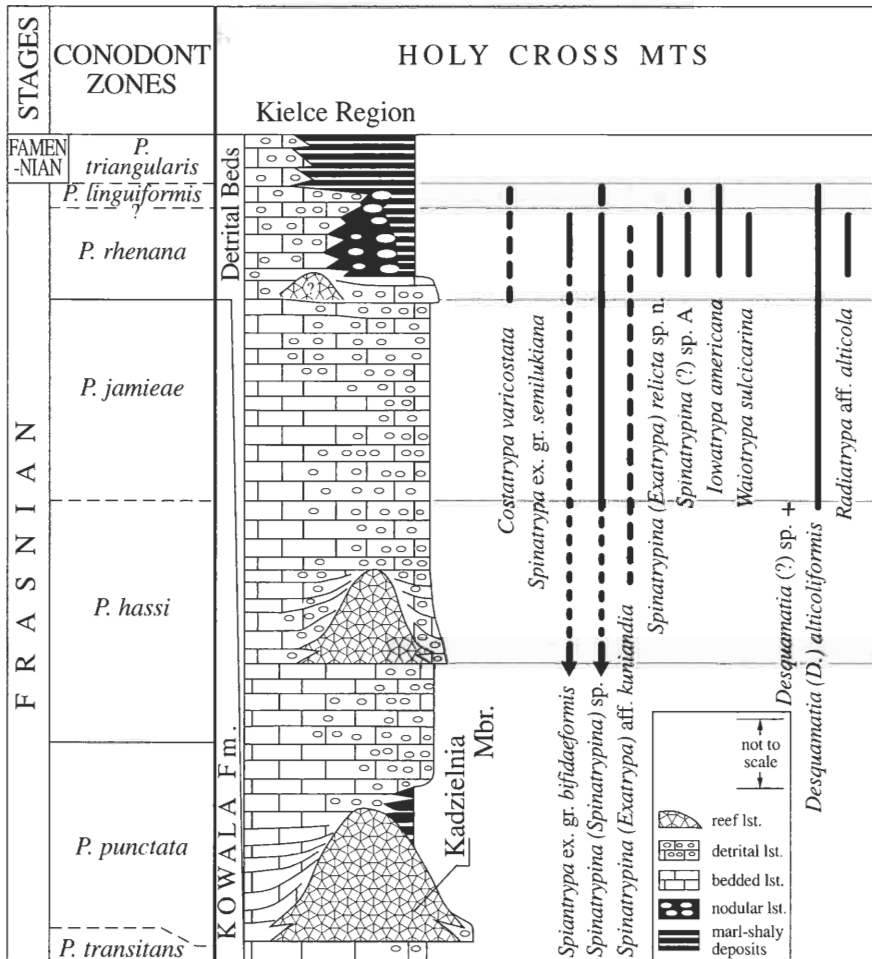


Fig. 17. Summarized Ranges of atrypid taxa in later Frasnian of the Holy Cross Mountains; *P.* – *Palmatolepis*.

Cycle (Fig. 2; see Narkiewicz 1988) was the local abundance of *Costatrypa* (Tudorów) and *Iowatrypa* (e.g., Miedzianka, Psie Górki). Atrypids occur also in allochthonous associations in downslope facies (Kadzielnia, Wietrznia; Kowala, see Miklas in Racki *et al.* 1993). Although stratigraphically older, the late Frasnian brachiopod faunas are marked by smaller shell sizes (Gawlik in Racki *et al.* 1993); a relatively large-sized *Desquamatia*(?) is the end-member of atrypid sequence at Psie Górki, continuing up to the F-F boundary (Fig. 16C). The average shell sizes of peri-reefal species are distinctly larger than those from non-reefal level-bottom populations, as shown within *Iowatrypa* (see Fig. 11). However, this shallow-water association is only tentatively determined in some sites, e.g., relatively large- and thick-shelled and coarsely-ribbed Variatrypinae (Fig. 16D) await specific evaluation.

Middle Frasnian deeper-water (level-bottom) faunas are marked by an undescribed *Pseudoatrypa* (Kowala, Wietrznia; *Phlogoiderhynchus polonicus* Assemblage; see

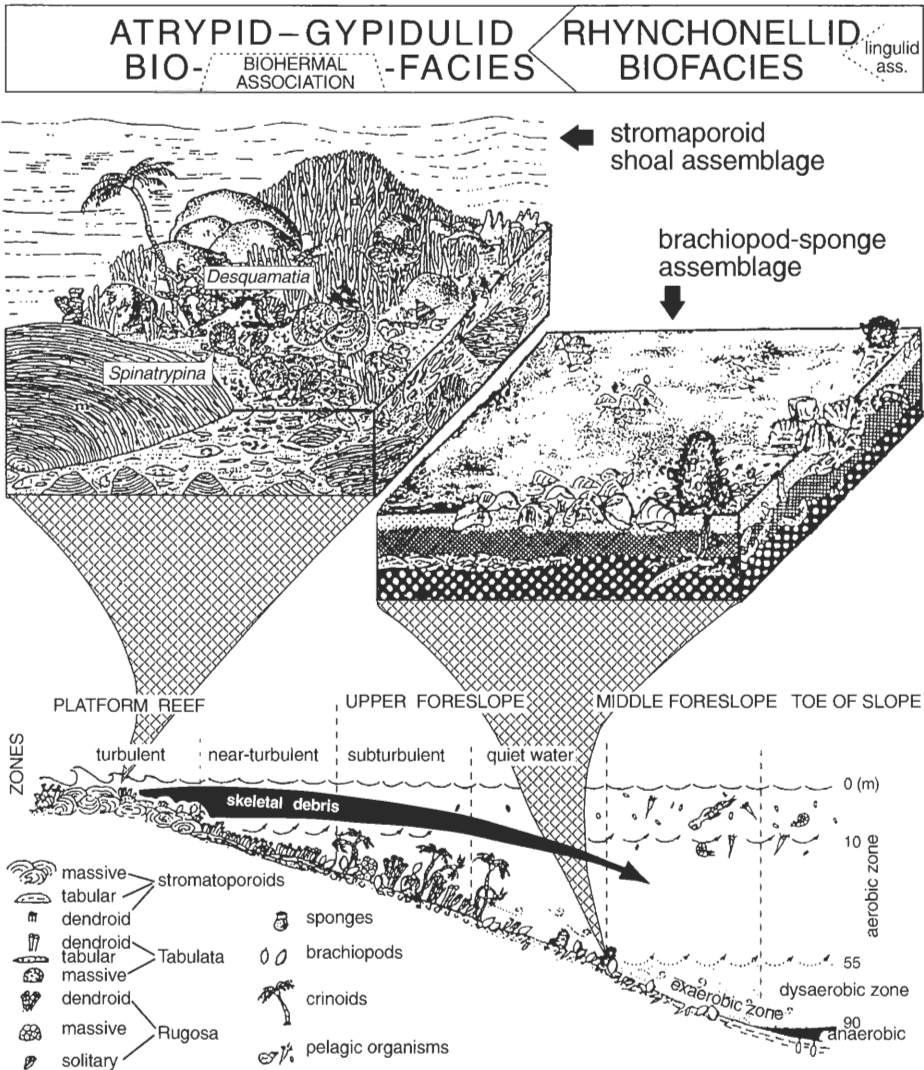


Fig. 18. Brachiopod biofacies model of the Frasnian reef of the Holy Cross Mountains (modified from Racki *et al.* 1993: fig. 14); atrypid and rhynchonellid brachiopods are shown as dominant element of two different communities developed in contrasting environmental setting.

Racki 1993a) or minute *Carinatrypa*(?) and *Spinatrypa* (see coeval faunas from Dębnik; Baliński 1979) during the initial IIc transgression (see Fig. 2). Higher in the sequences, quite abundant faunas with *Iowatrypa*, *Spinatrypina* (*Exatrypa*), *Costatrypa*, *Waiotrypa*, *Desquamatia* (D.) and *Radiatrypa* (see Fig. 17) were discovered at Kowala and Łgawa Hill in the lower part of the subset H-2. They occur primarily in at least two lumachelle horizons; thus the distinction between upper and lower foreslope assemblages remains ambiguous. Hence, rapid eustatic fluctuations, especially the basal IId eustatic rise (or the *Palmatolepis semichatovae* transgression; Sandberg *et al.*



1992) in the Early *P. rhenana* Zone, were coupled with a significant 'immigration' wave. The colonizers may have been recruited mainly from the Russian Platform, but western Laurussian connections are evidenced also by the appearance of the North American species *Costatrypa varicostata* and *Iowatrypa owenensis*.

The following transgressive/anoxic Lower KW Event in the Late *P. rhenana* Zone was without more catastrophic consequences for the brachiopod faunas in Poland. In contrast, the last phase of the deeper-water, downslope assemblages was clearly influenced by increased shallowing in later KW time, rapidly followed by expanding hypoxic conditions of the final deepening Ild pulse. Irregularly decreasing shell frequency is documented at Kowala toward the top of the subset H-2 (see Fig. 5). Dense storm-generated coquinaid intercalations (see also Miklas in Racki *et al.* 1993) are known ca. 15 m below the F-F boundary. The stratigraphically highest finding of *Costatrypa* and *Spinatrypina* is recognized 3.0 m below the F-F boundary, in the *Pammegetherhynchus* biostrome (*sensu* Aigner *et al.* 1977) within a more argillaceous unit. The assumed 'exaerobic' portion of the sequence probably represents an initial phase of the Upper KW Event, and, by inference, the *P. linguiformis* conodont Zone. This trend is associated with reorganization of the benthic and pelagic faunas in the very latest Frasnian interval (Racki 1993c: p. 9), concluding in the blooming of a siliceous sponge–radiolarian biota. The terminal collapse of the atrypids was coupled with the onset of episodic calcareous–biosiliceous deposition of the unit H-3, reflecting a severe eustatic fall in the F-F transition (Event 6 in Sandberg *et al.* 1988: p. 296), and corresponding apparently to the higher part of the Upper KW Limestone (Racki 1993c, 1996). Pre-extinction, transported brachiopod faunas have been found in a few crinoid-lumachelle lenticular streaks in this unit, and comprise several taxa (listed below), including a sporadic last atrypid *Iowatrypa*(?) (Fig. 5).

## Review of brachiopod faunas of the survival phase

The Polish Famennian brachiopod assemblages were living in rough-water habitats away from crinoid meadows and over the post-reef crest(s) (see summary in Biernat 1988). They are marked by an abundance of cyrtospiriferids, with some athyrids, productids, orthids and rhynchonellids (including large and distinctly ornamented *Zilimia*), known as early as the *Palmatolepis crepida* Zone (Biernat & Szulczewski 1993). In addition, low-diversity (sometimes monospecific) rhynchonellid faunas are known from different pelagic habitats (e.g., fauna with *Tenuisnurostrum subcrenulatum* Biernat, 1970), locally replaced by the small-sized smooth spiriferid *Nucleospira* and, especially, by inarticulates (*Orbiculoidea*) in the more hypoxic regimes (see also Żakowa & Radlicz 1990). Notable *Dzieduszyckia* shelly banks, regarded by some as associated with vent-seeps (Campbell & Bottjer 1995), are a peculiar character of the recovered Holy Cross Mountains biotas (see Biernat 1967). Biernat (1970) noted some atrypids from the early Famennian of Kadzielnia, but later sampling clearly shows that they were derived from the underlying Frasnian lithological members in this locality.

The deeper-water rhynchonellid-inarticulate biofacies is continuous across the F-F boundary (Figs 18, 19; see Racki *et al.* 1993). This is exemplified by the transition from *Ryocarhynchus tumidus* (Kayser, 1871) to *Orbiculatisinorostrum laeve* (Gürich, 1903) at the Łagów–Płucki section, and corresponding to the Dębik rhynchonellid faunas (Baliński 1979, 1995a). Furthermore, the relative advantage of inarticulates over articulates in the stressful setting is recorded in their prolonged ranges in the Kowala sections, in accordance with the selective survival model of Harries

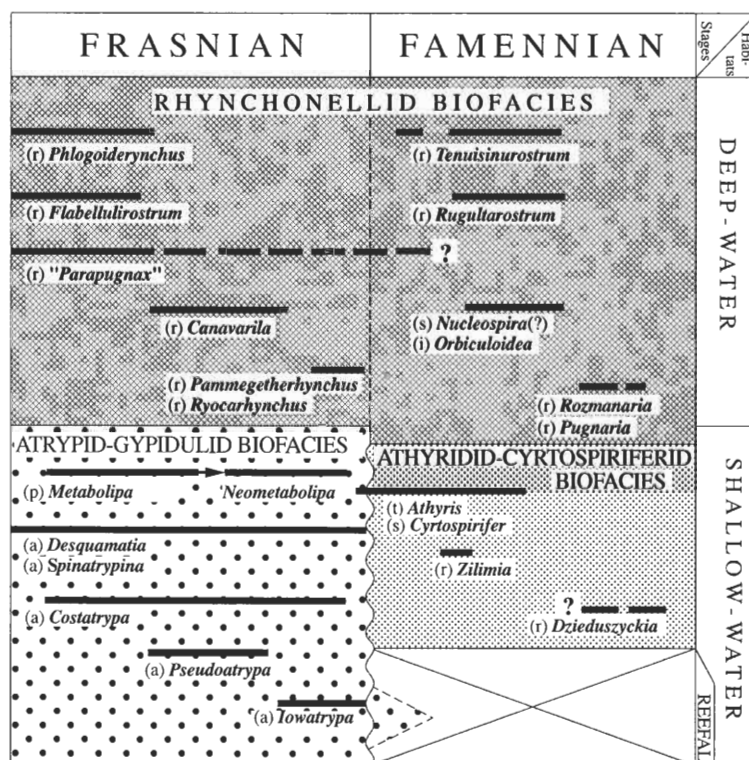


Fig. 19. Frasnian to Famennian brachiopod biofacies pattern in the Holy Cross Mountains (see also Fig. 18), with ranges of representative genera (after Racki *et al.* 1989: fig. 3; modified); a – Atrypida, p – Pentamerida, r – Rhynchonellida, s – Spiriferida, t – Athyridida, i – Inarticulata.

*et al.* (1996). In contrast, the replacement of the Atrypid–Gypidulid Biofacies by the athyridid–cyrtospiriferid faunas (Biernat 1988) is still poorly studied: these were largely disarticulated and reworked brachiopods (see Fig. 19).

Surviving brachiopod faunas were found in the F-F transition at Psie Górki and Kowala. At Psie Górki, localized coquinas were discovered in the latest *P. linguiformis* Zone, and were followed by the more widespread crinoid-shelly accumulations of the earliest Famennian, but probably belonging chiefly to the Middle *P. triangularis* Zone (units H-1a and H-1b, respectively; see Racki 1990). The impoverished latest Frasnian fauna (five genera only?) is dominated by *Schizophoria* and *Cyrtospirifer*, accompanied by *Douvillina*, smooth reticularid(?) spiriferids and rhynchonellids (*Ryocarhynchus*?). Notably, some atrypids and colonial corals were discovered in the topmost Frasnian. Stratigraphically the younger recovered assemblage is slightly more diverse (see Biernat 1988), but overwhelmingly dominated by *Cyrtospirifer*, *Schizophoria* and several productid species.

Allochthonous silicified pre-extinction faunas at Kowala (unit H-3; Racki 1993c) are characterized by many biernatellids (*Biernatella polonica* Baliński, 1977; see Baliński 1995a: p. 147) and other athyridids, schizophoriids, various spiriferids (mainly cyrtospiriferids and *Warrenella*?), small-sized orthids, *Productella*, and characteristic rhynchonellids comprising, among others, *Hypothyridina*- and *Ryocarhynchus*-like forms. The total generic diversity approaches ten (jointly with *Iowatrypa*?), but the composition of the particular shelly lenticular intercalations varies broadly. In fact, several brachiopod communities might be included in the ephemeral skeletal-intraclastic accumulations during at least two heavy storm events characteristic of this key timespan (tsunamis?; see Sandberg *et al.* 1988, 1992).

Cyrtospiriferid valve pavements are sporadic just above the F-F boundary at Kowala and Łgawa Hill. Cyrtospiriferid shell debris, with athyrids and schizophoriids, is also scattered in a thick conglomerate level at Śluchowice, corresponding to the *P. triangularis* Zone (see Fig. 3); in addition, a monospecific productellid (*Nigerinoplica*?) assemblage is also found in this interval. All the data suggest that these groups were a highly dominant component of the 'crisis zone' (*sensu* Harries *et al.* 1996), possibly including still some Frasnian survivors (as established among coeval crinoids; see Racki *et al.* 1989). Such biota are common in several sites of the Kostomłoty facies zone (Kościelniakowska 1967), where distinctive non-reef carbonate shoal deposits are developed (see Szulczewski 1971).

## Conclusions and final remarks

Rapid eustatic and climatic fluctuations (see Joachimski & Buggisch 1996), possibly coupled with oceanic hypoxic overturn and submarine volcanic/hydrothermal activity during the Upper KW Event (Racki 1996 in press), may have caused the demise of the low-latitude reef ecosystems, and of the associated shelly benthos. An irregular spatial pattern of extinction, as well as gradual repopulation of the drowned shoal, are evident from the vanished Dyminy Reef. A stepdown atrypid extinction (e.g., Copper 1986) is recorded in the sections, even though the late Frasnian brachiopod assemblages remain still diverse in the *P. rhenana* Zone, as established in the Łgawa Hill locality (at least 30 species; see Miklas in Racki *et al.* 1993), and comparable in this respect to the rich Kadzielnia bioherm association (Biernat 1971). Atrypids were also still dominant among upper slope faunas, and at least 13 species persisted in the early interval of the KW Crisis (Fig. 17). This diversity is also similar to (or even higher than) that of faunas from the older Frasnian levels (see Racki 1993a: fig. 33). An affinity of the late Frasnian atrypids with Russian, as well as with North American and western Australian faunas is notable, albeit in combination with some degree of endemism (known for the older biotas; Racki 1988). A refugial character is also noted by Grey (1978) for atrypids from the Australian reef complex.

As in the gypidulids (Godefroid & Racki 1990), the last developmental phase of the atrypids is characterized by a distinctive set of genera and species, especially among the Spinatrypinae and Pseudogruenewaldtiinae (Fig. 17). Middle Frasnian brachiopod faunas are relatively poorly studied, thus this is still a gap in our knowledge of evolutionary lineages traced from the early Frasnian. Towards a fuller understanding of the late Frasnian bio-crisis, the next stage of integrative ecostratigraphic study should be focused on both the pre-crisis (middle Frasnian) and succeeding (Famennian) faunas. The biogeographic pattern within the Laurussian shelf also remains enigmatic, although a southward extension of some rhynchonellid assemblages from the eastern Holy Cross Mountains is already obvious (see Sartenaer *et al.* 1998). Northern (Łysogóry) basin faunas await recognition too, but this is probably possible only in boreholes.

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## Appendix 1

### Late Frasnian atrypid localities

All the accessible exposures (for details of locations see ‘Register of localities’ in Racki 1993a), grouped mostly in the western part of the Holy Cross Mountains, have been examined. However, the most complete sections of Kowala-Łgawa Hill and Psie Górki are presented below in greater detail (Fig. 4), as the reference succession for the basin and near-reef (foreslope) settings, respectively.

**Kowala.** — The atrypid sites are scattered on a hill south of the village of Kowala. The main source outcrop is situated at the western end of the hill, presently intersected by an industrial road cutting, linking the Nowiny cement factory with the Kowala Quarry (Miklas in Racki *et al.* 1993: pl. 1). Farther to the east, the late Frasnian strata are well exposed in the nearby railway cutting (reference section, described by Szulczewski, 1971) and Kowala (formerly Wola) Quarry. In the active quarry, the Late Devonian sequence, more than 350 m thick, is exposed on the gently dipping southern limb of the Gałęzice Syncline (Figs 3–5). Additional data come from the borehole Kowala 1, located 500 m to N of the Kowala Quarry (Romanek & Rup 1990).

This well-known, continuous succession of the Chęciny–Zbrza basin (see summary in Racki 1993c) was the principal reference composite section for the biostratigraphic analysis of the last

atrypid occurrences, although the brachiopod collection from the laterally changing late Frasnian strata is not particularly large.

Within the dark to black, bituminous marly series, four units are distinguished in the F-F transition beds (H-1 to H-4; Fig. 5), as proposed previously for the Jaźwica section (Racki & Zapaśnik 1979: fig. 3). The descriptions below are based mainly on the eastern walls of the quarry (see Racki 1993c, 1996):

H-1. Variably bedded fossiliferous marly-micritic sequence, up to 12 m thick, contains intercalations of graded detrital limestones (with broken reef-builders) and thick (up to 1 m) slump layers. Changing wavy bedding, with a gradual transition into a nodular fabric, characterized several parts of the unit. Silicified brachiopod coquinas, with many atrypids, are infrequent, associated with diverse corals and rare silicisponges.

H-2. Thin- and rhythmically-bedded marly limestones and shales, up to 17 m thick, comprise frequent irregular subnodular and nodular intercalations, up to 45 cm thick. A few planar-bedded laminated beds and shale horizon, 25–40 cm thick, mark the top of the unit. The fossil assemblage is less abundant than in the underlying unit. It includes both planktic and benthic elements, with homotenenids and rhynchonellid brachiopods (mostly *Pammegetherhynchus*; Sartenaer *et al.* 1998) in a leading role, and amphiporid branches common in some beds; atrypids occur only sporadically.

H-3. Platy limestones, with beds up to 50 cm thick, and thinner (usually less than 5 cm) shale interstratifications. This calcareous-cherty unit, 6 to 8 m thick, is the main departure from the otherwise uniform marly succession. The beds are composed of variably alternating radiolarian-spiculitic micritic and 'grained' (sparstone) bands and partings, giving a crude laminated to ribbon appearance. Coquinite-crinoid lenticular accumulations (with the last atrypids) occur particularly in the middle portion of this unit.

H-4. Thick monotonous series, above 100 m thick, of thin- and rhythmically-bedded marly limestones and shales (Marly Facies of Szulczewski 1971). With the exception of sporadic bioclastic, mainly crinoidal partings, the impoverished macrofauna is limited to *Guerichia* and largely inarticulate brachiopods (see Żakowa & Radlicz 1990).

Units H-1 and H-2 certainly belong to the *P. rhenana* Zone, but the upper boundary of this zone is poorly established. The recognized entry of *P. linguiformis* in the uppermost part of set H-2 is probably facies controlled, and records only the advance of the transgression pulse. The F-F boundary is placed in the lower segment of unit H-3, but at varying levels: about 2.5 m above its base in the eastern wall, whilst only 1.3 m above the base in the central part of the quarry.

The well-known railway cutting succession is marked by a scarcity of brachiopods in its upper, marly part (unit H-2), but several, mostly rhynchonellid-dominated, faunas were obtained from the older units (e.g., Sartenaer *et al.* 1998). The road cutting section, through the westernmost part of the Kowala outcrop, comprises mostly various detrital lithologies, with a gradual transition into a marly rhythmic set (unit IV of Miklas in Racki *et al.* 1993). The associated silicisponges (Rigby *et al.* in preparation) were the obvious source for the intensive silicification. Numerous silicified atrypids have been collected, mostly from the middle units (units II–II), but predominantly from loose material. Therefore, only crude stratigraphic ranges have been established, and the atrypid fauna can be assigned only to the undivided *P. rhenana* zonal interval (?mainly the Late *P. rhenana* Zone).

**Łgawa Hill (eastern Jaźwica).** — The principal part of the material under study was collected in the active Jaźwica quarry on the Łgawa Hill, south of the village of Bolechowice, located ca. 3.5 km to the west from Kowala (Racki 1981). The abundant material was found almost exclusively as weathered loose specimens and in rock slabs, chiefly from the talus along the north-eastern wall. Unfortunately, only sporadic brachiopod specimens were collected in situ, seriously hindering the stratigraphic and ecologic analysis, although this deficiency is alleviated in view of the good correlation with the Kowala exposures.

Infrequent brachiopod bioclastic intercalations, within thin (up to 10 cm) layers of irregularly banded to nodular, grey or cherry-reddish weathering marly limestones, are the most abundant source of the atrypids and other diverse brachiopods (see Miklas in Racki *et al.* 1993: table 1). These strata are part of the interbedded shaly-lime sequence, with black cherts (marly-detrital unit R of Racki 1981; equivalents of the unit H-2 from Kowala; see Racki & Zapaśnik 1979: fig. 3); these sediments



were probably originally dark to black, as seen in the levels being exploited in the Kowala Quarry. In terms of conodont zonation, the atrypids and other diverse fauna (e.g., Wrzolek, 1988; Rigby *et al.* in preparation) are limited to the *P. rhenana* Zone (?mostly its later part). Transition to the overlying well-bedded unit S (= H-3) is now very well exposed, and the study of the F-F passage has also revealed a few thin shelly intercalations.

**Psie Górki.** — Several small abandoned and partly overgrown quarries are located on the southern slope of the hill in the middle part of the Kadzielnia Chain, in the southern part of Kielce (Szulczewski 1971).

The late Frasnian to oldest Famennian sequence of Psie Górki is subdivided into seven lithologic sets (C-I) comprising almost exclusively different detrital limestones of the fore-reef facies (Fig. 3; see description by Gawlik in Racki *et al.* 1993), on the northern margin of the Dyminy Reef. Older Frasnian stromatoporoid and coral limestones (sets A–B; Racki 1993b) crop out on the adjacent Cmentarna Góra hill.

The section is characterised by a gradual upward decrease in the macrofossil content, chiefly reworked reef-builders. Equivalents of the Lower KW Event cannot be recognized within the rapidly deposited upper-slope sediments, which probably correspond largely to the reef-cap stage (Narkiewicz 1988). The most significant facies change corresponds to the contact between sets G and H (see details in Racki 1990, 1993b), close to the F-F boundary. Mostly coarse-grained and intraclast-enriched limestones with still diverse fossils (including crinoid-brachiopod atrypid-bearing horizons) are abruptly replaced upward by more fine-grained deposits containing crinoid debris, and enriched westwards in brachiopod and nautiloid shelly intercalations (bed H-1b). The micritic bottom level (H-1a) displays impoverished skeletal content, but also the highest occurrences of corals and atrypids; the layer most probably still belongs to the *P. linguiformis* Zone. In the higher part of the set, well-sorted intrabiosparites occur, mostly representing the Middle *P. triangularis* Zone. Thus, significant condensation (maybe a small gap?) is apparent in this part of the succession.

**Other atrypid localities.** — Frasnian brachiopod-bearing successions, distributed along the Kadzielnia Chain, have been described by Godefroid & Racki (1990). The significant, because relatively well preserved, atrypid material, was collected at a small disused quarry at Grabina. Atrypid-rich lumachelle 'nests' are dispersed within light-coloured, poorly-bedded fine-grained deposits (set B in Racki 1993a) containing small cyanobacterial-*Stachyodes* buildups; the strata represent the undivided Late *Palmatolepis hassi* - *P. rhenana* zones (see also Wrzolek 1988). The brachiopod-rich Tudorów locality near Opatów, in the eastern Holy Cross Mountains (Samsonowicz 1917), was also described by Godefroid & Racki (1990). Numerous, mostly articulated atrypids have been collected from the largely overgrown minute rural quarry. Brachiopod coquina is embedded in partly dolomitised, light-coloured 'reefal' limestones, roughly dated with macrofauna and conodonts as probably Early *P. rhenana* (?and/or *Palmatolepis jamieae*) Zone.

The well-known late Frasnian successions at Kadzielnia and Wietrzna in Kielce, predominantly various biotrital, partly talus-like deposits (Szulczewski 1971; Racki *et al.* 1993), are marked by extensively reworked shelly material. Macrofaunas are reported rarely from other late Frasnian localities, such as Śluchowice, Miedzianka, Sobiekurow, Kostomłoty, Domaszowice, Łagów-Plucki and Włochy-Nieczulice. In fact, only sporadic and mostly poorly preserved atrypids have been collected from the variously developed successions, although other brachiopods are quite abundant in some lumachelle intercalations.